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Cover: The Middle Ordovician trilobite *Ogygiocarella* from Builth was one of the first fossils described from Britain, being figured by Edward Lhwyd in 1698.

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SYSTEMATICS OF THE OLIGOCENE TO MIOCENE REEF CORAL *TARBELLASTRAEA* IN THE NORTHERN MEDITERRANEAN

by ANN F. BUDD, FRANCESCA R. BOSELLINI *and* THOMAS A. STEMANN

ABSTRACT. Multivariate statistical analyses are used to distinguish species of the common reef-building coral *Tarbellastraea* at Oligocene and Miocene localities within the Aquitaine Basin, western Mediterranean, and central Paratethys regions; and to trace their distributions through geological time. Thirteen measurements or counts are made on thin sections of 126 colonies collected at 13 widely scattered localities, whose geological ages are newly updated. The data are analysed using average linkage cluster analysis and canonical discriminant analysis to distinguish clusters of colonies representing morphometric species. Names are assigned by qualitatively comparing measurements on the statistically recognized species with those of primary types of all previously described species of *Tarbellastraea*.

The results show that *Tarbellastraea* originated during the Oligocene (Rupelian) and became extinct during the Early Messinian. A total of 12 species (including two new species from the Italian Oligocene, and two species described previously as varieties) lived in the investigated areas during Oligocene and Miocene time. Except during the Oligocene, all but one species (*T. ellisiana*) were widespread. Although species richness within the genus remained constant at 5–7 species throughout much of its stratigraphical range, morphological disparity decreased significantly through time. The observed constancy in richness contrasts with the decrease reported overall in the Mediterranean reef coral fauna. Species originations were highest during the Burdigalian, when temperatures across the region increased. Species extinctions remained constant until the latest Miocene, when the extinction rate increased as cold Atlantic waters entered the Mediterranean.

New species described are *Tarbellastraea bragai*, *T. chevalieri*, *T. russoi* and *T. salentinensis*.

The extinct scleractinian genus *Tarbellastraea* Alloiteau, 1950 was one of the predominant reef-building corals on Mediterranean reefs during the Miocene (Chevalier 1962). During the Early and Mid Miocene, it was abundant in the diverse but small buildups that prevailed across the Mediterranean (Monleau *et al.* 1988) and European Atlantic regions (Cahuzac and Chaix 1993). During the Late Miocene, *Tarbellastraea* was one of two key framework builders of the large, well-developed reef systems that developed in the western Mediterranean (Esteban 1979; Martin *et al.* 1989; Pomar 1991). Despite the importance of *Tarbellastraea*, no stable taxonomy currently exists for distinguishing 'species' within the genus, and its stratigraphical duration and geographical range are debated. As a consequence, the evolutionary history of *Tarbellastraea* is poorly known.

Although several species of *Tarbellastraea* were described by authors in the nineteenth century (e.g. Reuss 1847, 1872; Milne Edwards and Haime 1850), the most comprehensive treatment of the systematics of the genus was that of Chevalier (1962). Chevalier (1962) described 12 species (five new) and seven varieties (six new) of Miocene western Mediterranean *Tarbellastraea*. He distinguished these species qualitatively using a large number of skeletal features, including colony shape, calice shape, calical relief, calice size, number of septa per corallite, columella structure, relative development of the primary and secondary septa, and calice spacing. His work was later questioned by taxonomists studying environmental variation in living Indo-Pacific species, because many of the features used by Chevalier (1962) had been found to vary widely in response to the environment (Best *et al.* 1984). Because of overlap among species in measurements made on corallite diameter, calice spacing, and number of septa per corallite, Oosterbaan (1988) synonymized five of the species recognized by Chevalier (1962) in the Burdigalian of the Aquitaine Basin. Best *et al.*

(1984) further suggested that the overlap indicated that all of the species and varieties treated by Chevalier (1962) were probably only one species, *Tarbellastraea ellisiana* (Defrance, 1826).

Recent work on living Caribbean species of the closely related genus *Montastraea*, however, has shown that morphological differences among species may be much more subtle than previously appreciated, and that morphological overlap among species may be common in closely related species (Knowlton *et al.* 1992; Weil and Knowlton 1994). Three electrophoretically distinct sibling species within the *Montastraea annularis* complex differ primarily in morphological characters (involving colony form and calical relief) that have high environmental variation (Knowlton *et al.* 1992; Weil and Knowlton 1994). Nevertheless, sibling species within the complex can be distinguished morphometrically by applying multivariate statistical methods to measurements made on colonies from populations collected in different environments (Budd 1993). The statistical results show that no single character can be used to distinguish species within a complex, but ten or more characters must be considered in concert. Different types of morphological features are needed to distinguish species in different cases.

In this paper, we revise species of *Tarbellastraea* in some Mediterranean and European basins using a similar morphometric approach, derived from the methods of Budd and Coates (1992) and Budd (1993). Our approach is stratophenetic (*sensu* Gingerich 1979), and involves: (1) taking a number of linear measurements and counts on colonies in sample populations collected at a wide range of localities; (2) using multivariate statistical procedures, including cluster analysis and canonical discriminant analysis, to group colonies within pre-defined stratigraphical levels into clusters; and (3) statistically linking clusters into 'morphometric species' to trace their ranges through geological time. Comparisons are made with primary types, and names are assigned only after morphometric species have been recognized statistically. Because the approach is based on quantitative analyses of sample populations (i.e. > 5 colonies from any one locality), some of the difficulties associated with recognizing discrete morphological entities or 'morphometric species' in highly variable organisms, such as corals, are reduced.

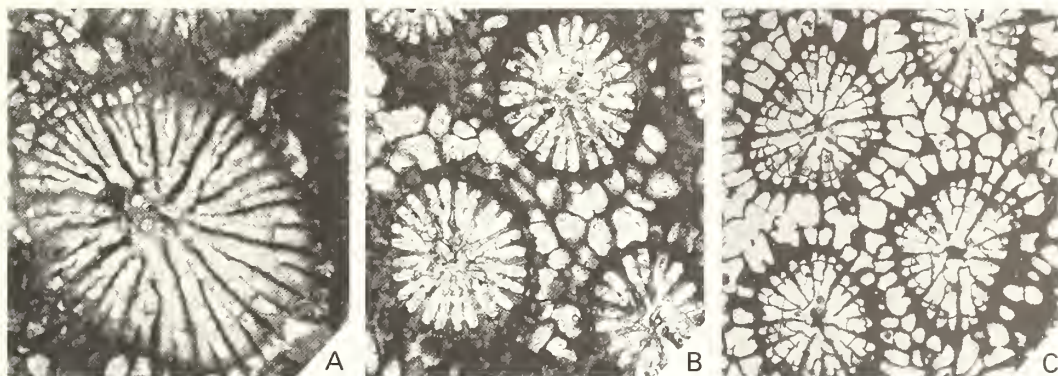
Our aim in this paper is to provide a consistent taxonomy that can be used to identify species of *Tarbellastraea*. Our work is unique in its focus on a single Mediterranean genus. It also considers several pre-Miocene occurrences of the genus, some of which are recorded for the first time. Like Chevalier (1962), as part of our revision, we interpret species origination and extinction events by considering the palaeogeography of the region. However, unlike Chevalier (1962), our interpretations are made within the context of updated higher resolution stratigraphies and current paleogeographical reconstructions. In the future, we plan to continue our study of *Tarbellastraea* by treating material from northern Africa and the Middle East, so that we can eventually examine evolutionary relationships among species. We believe that a thorough revision of the species of *Tarbellastraea*, as begun here, is an essential first step in reconstructing any meaningful phylogeny of the genus.

DIAGNOSTIC CHARACTERISTICS OF *TARBELLASTRAEA*

Because very little molecular or phylogenetic work has been done on scleractinian corals, most established Cenozoic genera have been defined on the basis of skeletal characters, that are easy to observe on upper calical surfaces (see Vaughan 1907; Lang 1984, for discussion). Using the morphological terminology of Wells (1956), in colonial scleractinians (except the suborder Astrocoeniina), species are generally distinguished by the architecture of the individual corallites (e.g. corallite diameter, number of septal 'cycles' *sensu* Wells 1956, fig. 240); whereas genera are distinguished by the degree of integration of corallites within colonies (e.g. plocoid *vs* cerioid colony forms, wall structure, development of costae), and by the development of the columella (Budd 1990).

Although *Tarbellastraea* was first designated as a new genus by Alloiteau (1950), its morphology was not described in detail until Alloiteau (1952) emphasized the small corallite diameter, often

'parathecal' wall structure, tabulo-vesicular coenosteum, and commonly lamellar columella of the new genus. Many of these characteristics are also possessed by seven other plocoid genera (Table 1), which, like *Tarbellastraea*, belong to the family Faviidae Gregory, 1990; differences between these eight genera are often difficult to detect without detailed microscopic examination. Nevertheless, with the exception of *Antiguastrea* Vaughan, 1919, *Tarbellastraea* is unique in its possession of a lamellar columella and a distinctive para- to septothecal wall structure. In both genera, the wall is primarily septothecal (i.e. formed by the thickening of the outer part of the septa), but it is sometimes reinforced by additional dissepiments, which are characteristic of true 'parathecal' walls (*sensu* Wells 1956, fig. 245). Two genera (*Plesiastrea* (*Palaeoplesiastrea*) and *Solenastrea*) contain species that resemble species of *Tarbellastraea* in almost every detail, except that they have spongy columellae and weak costae (Text-fig. 1).



TEXT-FIG. 1. Transverse thin sections of *Tarbellastraea* and two morphologically similar genera showing the differences in wall structure, columella form, and number of septal cycles among genera. A, *Antiguastrea cellulosa* (Duncan, 1863), type species of *Antiguastrea* Vaughan, 1919; SUI-84922-G; Upper Oligocene, Guayanilla, Juana Diaz Formation, Puerto Rico (Realini collection). B, *Solenastrea* sp.; SUI-84921-A; Langhian, Neffies, Languedoc, France (with the exception of its spongy columella, this species is almost identical morphologically to *T. reussiana* which occurs at the same locality). C, *Tarbellastraea ellisiana* (Defrance, 1826), type species of *Tarbellastraea* Alloiteau, 1950; SUI-84740-A; Lower Burdigalian, Cabanes, Saint-Paul-les-Dax, Bordeaux (France). All $\times 8$.

The primary morphological differences between *Tarbellastraea* and *Antiguastrea* are similar in nature to differences that typically distinguish species. Species of *Tarbellastraea* usually have smaller corallite diameters and fewer septal cycles than species of *Antiguastrea*; however, clearly there is overlap (e.g. *Antiguastrea prava* Budd *in* Budd *et al.* 1992, from the Eocene of Panama, which has a corallite diameter of 3–4 mm and three cycles of septa). Nevertheless, the absence of *Antiguastrea* (as delineated in Table 1) from any of the Miocene units described herein (Chevalier 1962) suggests that vast majority of the species of *Tarbellastraea* in the present study may be descended from a common ancestor, and thus had an evolutionary history distinct from that of *Antiguastrea*. As mentioned above, studies similar to the present one are needed on (1) *Tarbellastraea* from the south-western and eastern Mediterranean and the Middle East and (2) *Antiguastrea* from the Mediterranean and the Caribbean regions, before a rigorous phylogenetic analysis can be performed to assess the taxonomic validity of distinguishing *Tarbellastraea* from *Antiguastrea*.

TABLE 2. Collecting localities for samples used in the morphometric analysis and their geological ages.

Locality	Abbreviation	Number of colonies measured	Age	Age reference
1. Vitigliano (Salento Peninsula, Apulia, Italy)	SP	8	Mid Chattian	Bosellini and Russo 1992
2. Carry-le-Rouct (La Nerthe, Bouches-du-Rhône, France)	NE	16	Late Chattian	Monleau <i>et al.</i> 1988; Nury 1994
3. Dolianova (Cagliari, Sardinia, Italy)	SR	4	Late Chattian-Aquitania	Cherchi and Montadert 1984
4. Eggenburg (Vienna, Austria)	EG	10	Eggenburghian (i.e. Early-Mid Burdigalian)	Steininger and Senes 1971; Steininger <i>et al.</i> 1990
5. Cabanes (St.-Paul-lès-Dax, Landes, France)	DX	10	Early Burdigalian	Cahuzac and Poignant 1992; Cahuzac and Chaix 1993
6. Le Peloua and Mérignac (Bordeaux, Gironde, France)	LP	28	Early Burdigalian	Poignant and Pujol 1978; Cahuzac and Chaix 1993
7. Sciolze, Termô Fôrâ, Albugnano, (Torino, Piedmont, Italy)	TO	5	Burdigalian-Langhian	Bonsignore <i>et al.</i> 1969; Clari <i>et al.</i> 1994
8. Leibnitz (Graz, Austria)	GR	5	Early Badenian (i.e. Langhian)	Friebe 1991a, 1991b
9. Pleven (Bulgaria)	BL	11	Early Badenian (i.e. Langhian)	Kojumdzieva <i>et al.</i> 1978
10. Autignac, Neffies and Serrière, (Beziers, Languedoc, France)	LD	13	Langhian	Magné 1978
11. Landro and Nicosia (Sicily, Italy)	SI	3	Late Tortonian	Catalano 1979; Grasso and Pedley 1988
12. Purchena and Los Marmoles (Almería, Spain)	AL	9	Late Tortonian	Martin <i>et al.</i> 1989
13. Cala Pi (Mallorca, Balearic Islands, Spain)	MA	5	Late Tortonian- ?Early Messinian	Pomar 1991, 1993

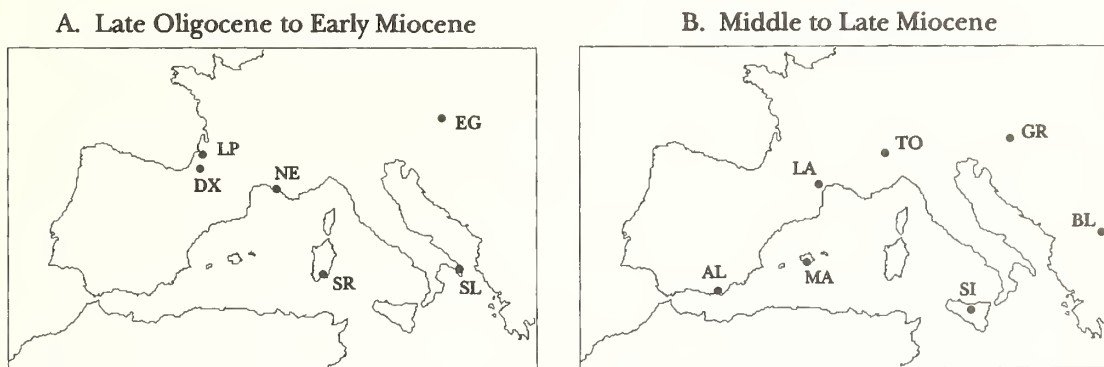
TABLE 1. Comparison of diagnostic morphological features in *Tarbellastraea* with those in morphologically similar genera (after Vaughan and Wells 1943; Wells 1956; Chevalier 1962). Following Vaughan and Wells (1943), synonyms for the genus *Montastraea* include: *Orbicella* Dana, 1846; *Phyllocoenia* Milne Edwards and Haime, 1848; and *Helastrea* Milne Edwards and Haime, 1857.

Genus	Colony form	Corallite diameter	Wall structure	Septal cycles	Palifom lobes	Columella	Exotheca
1. <i>Tarbellastraea</i> Alloiteau, 1950	Plocoid	< 3.5 mm	Para- to septothecal	3-4 cycles	Weak or absent	Sublamellar to lamellar	Weak costae, tabularo- vesicular coenosteum
2. <i>Antiguastrea</i> Vaughan, 1919	Subplocoid- plocoid	> 3.5 mm	Para- to septothecal	3-5 cycles	Weak or absent	Lamellar	Weak costae, tabularo- vesicular coenosteum
3. <i>Cyphastrea</i> Milne Edwards and Haime, 1848	Plocoid	< 2.5 mm	Septothecal	2-3 cycles	Weak to strong	Papillose to spongy	Very weak costae, spinose coenosteum
4. <i>Leptastrea</i> Milne Edwards and Haime, 1848	Subcerioid- plocoid	2-11 mm	Septothecal	2-5 cycles	Weak	Papillose	Weak costae, dense coenosteum
5. <i>Montastraea</i> de Blainville, 1830	Plocoid	> 2.0 mm	Septothecal	3-4 cycles	Weak or absent	Spongy	Strong costae, tabular coenosteum
6. <i>Solenastrea</i> Milne Edwards and Haime, 1848	Plocoid	< 3.5 mm	Septothecal	3 cycles	Weak	Papillose to spongy	Very weak costae, vesicular coenosteum
7. <i>Plesiastrea</i> Milne Edwards and Haime, 1848	Plocoid	> 2.0 mm	Septothecal	3 cycles	Strong (rudimentary inner fan system)	Papillose to spongy	Strong costae, tabular coenosteum
8. <i>Plesiastrea</i> (<i>Palaeoplexistrea</i>) Chevalier, 1961	Plocoid	< 3.5 mm	Septothecal	3 cycles	Weak	Papillose	Very weak costae, vesicular coenosteum

RECOGNITION OF SPECIES USING MORPHOMETRIC METHODS

Material

A total of 127 colonies of *Tarbellastraea* was selected for analysis from collections made at 13 localities (Text-fig. 2; Table 2). All of the colonies were relatively well preserved and possessed the diagnostic criteria outlined above. The 13 localities are widely scattered across the Aquitaine Basin, western Mediterranean, and central Paratethys regions, and include the type localities for 14 of the 25 previously described species and varieties of *Tarbellastraea*. The localities consist of a range of different reef settings, including reef-complexes with lagoonal patch reefs (MA, SI), fringing reefs and patch reefs (SP, NE, DX, LP, GR, LD, AL), and smaller buildups (SR, BL). Two scattered coral horizons (EG, TO), in which true reef framework was not formed, have also been considered.



TEXT-FIG. 2. Maps showing 13 collecting localities. Abbreviations for localities are given in Table 2.

Most of the collections were made recently by either A. F. Budd (14 colonies at NE, 10 at EG, 10 at DX, 10 at LP, 5 at GR, 11 at BL, 11 at LD), F. R. Bosellini (8 colonies at SP, 5 at MA), J. C. Braga (9 colonies at AL), or A. Russo (4 colonies at SR). However, 30 additional specimens (2 colonies at NE, 18 at LP, 5 at TO, 2 at LD, 3 at SI) were selected from collections made by the late J. P. Chevalier and his predecessors at the Institut de Paléontologie, Muséum National d'Histoire Naturelle, in Paris, France (MNHN, I.P.). Wherever possible, at least ten colonies were selected from each locality; however, in the case of six localities, fewer specimens were available for analysis because of inadequate preservation (Table 2).

Six other localities where primary types of species and varieties of *Tarbellastraea* have been found include: the Vicentin area of northern Italy (Rupelian), the Landes region of southern France (Stampian), the Touraine region of north-west France (Langhian), the Vienna Basin of Austria (Badenian), the Granada region of Spain (Late Tortonian), and Malta (Late Tortonian to Early Messinian). The geographical proximity of (1) the Vienna localities to localities of similar age and environment in the Styrian Basin (GR; Table 2) and (2) the Granada localities to localities of similar age and environment in Almería (AL; Table 2), indicates that two of the six faunas may be partially represented in our present samples.

In order to determine geological age dates for the 13 localities, one of us (FRB) consulted with specialists on the local geology of each area, and conducted a thorough review of the most recent literature. The findings are summarized in Table 2. Age dates for the 13 localities vary in quality. In some cases (e.g. NE, DX, LP, EG, GR), microfossils have been rigorously investigated using up-to-date biostratigraphical methods. In others (e.g. SR, TO, LD), very little recent biostratigraphical work has been done. A second paper is currently in progress discussing these stratigraphical problems and the reef settings in fuller detail.

Because of the tendency for repeated evolution of similar morphologies over geological time within many scleractinian coral lineages (see Budd and Coates 1992), the 13 localities have been

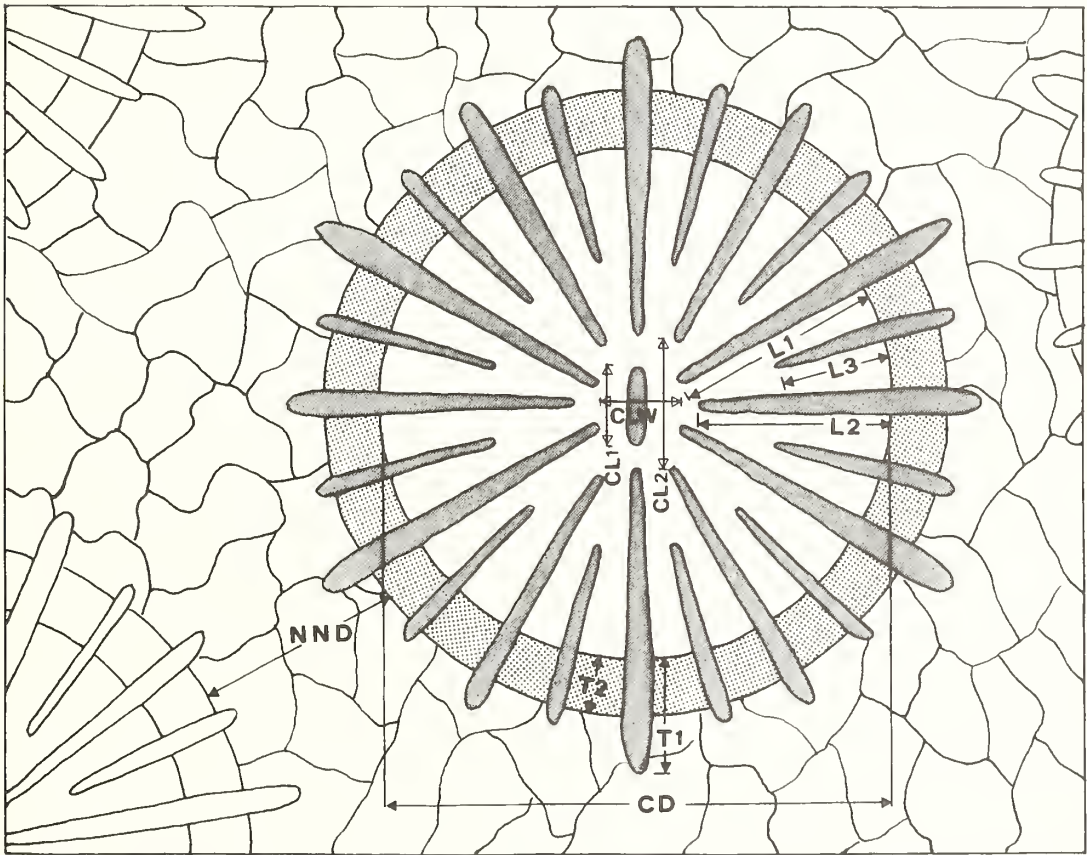
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8. Leibnitz (Graz, Austria)	GR	5	Early Badenian (i.e. Langhian)	Friebe 1991a, 1991b
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13. Cala Pi (Mallorca, Balearic Islands, Spain)	MA	5	Late Tortonian- ?Early Messinian	Pomar 1991, 1993

subdivided into two major groups for the purposes of the statistical analyses: (1) Late Oligocene to Early Miocene (SP, NE, SR, EG, DX, LP, TO), and (2) Middle to Late Miocene (GR, BL, LD, SI, AL, MA). Because clusters of colonies are distinguished in our protocol only at the initial stages in analysis and subsequently linked together to form morphometric species, temporally subdividing the material in this way serves to reduce the overall number of taxa and evolutionary intermediates, and thereby enhances resolution at the critical initial stages of analysis when cluster nuclei are first detected. This procedure improves the capability for discriminating morphologically similar clusters that would otherwise intergrade and be less distinct in an all-encompassing statistical analysis of material from all localities and ages.

Characters

A total of 12 linear distances was measured on transverse thin sections of five to ten well-preserved corallites per colony (Text-fig. 3). The total number of septa ('NS') was also counted on each measured corallite. Measurements were only obtained from mature corallites on each colony.



TEXT-FIG. 3. Diagram showing nine of the 12 characters measured on transverse thin sections: CD (= CD-MIN), minimum corallite diameter; CL1, columella tubercle length; CL2, CLW, corallite centre width; L1, septum length (1st cycle); L2, septum length (2nd cycle); L3, septum length (highest cycle); NND, distance between corallites; T1, costa length; T2, theca thickness. Three additional characters that were measured were: CD-MAX, maximum corallite diameter; ST1, septum thickness (first cycle); ST2, septum thickness (second cycle). All measurements were made to the nearest 0.01 mm. On poorly preserved colonies, only CD-MIN, NND, and T2 were measured.

Corallites were judged to be mature if their highest septal cycle was relatively well-developed.

In general, these characters estimate the sizes of various corallite architectural features, and the size and spacing of corallites. They were selected because they represent a minimal set of diagnostic characters within a larger suite of characters used in previous morphometric work on fossil and living species of *Montastraea* (Budd 1991, 1993), a closely related genus which shares almost all of the same features (Table 1). In this previous work, morphometric species recognized using methods similar to those in the present study were found to correspond well with biological species recognized using molecular data. A few previously used morphometric characters of *Montastraea*, including several measurements related to skeletal density, spacing and trabecular thickness, could not be measured in the present study because of inadequate preservation. These measurements are sometimes taken more accurately in longitudinal section. Characters measured in the present study that are unique to *Tarbellastraea* include the dimensions of the columella tubercle (CL1, CL2), the thickness of the parathecal wall (T2) and costa length (T1).

The measurements and counts used in the present study are similar to those used by Chevalier (1962). However, again, as mentioned above, because of inconsistencies in preservation, not all of the characters treated by Chevalier (1962) could be measured, and analysed statistically. No measurements could be made of calical relief, or of the structure and development of the endo- or exotheca. Similarly, no measurements were made of overall colony size or shape. These characters are, however, treated qualitatively in the species descriptions.

Moreover, on some corallites, only some of the 12 characters (Text-fig. 3) could be measured, due to inadequate preservation. This is especially true of colonies from SP and SR, on which measurements of septal thickness (ST1, ST2) could not be reliably obtained. Because of missing data in these cases, morphological clusters were first distinguished by analysing only data from well-preserved material. Data from less well-preserved material were subsequently compared statistically with these initial morphological clusters.

In sum, the characters measured and statistically analysed in the present study are not the only characters that can be used to distinguish the species studied. They merely represent the characters with high species diagnostic potential based on previous work, and characters that could most easily and consistently be measured on the largest number of colonies in the assembled material.

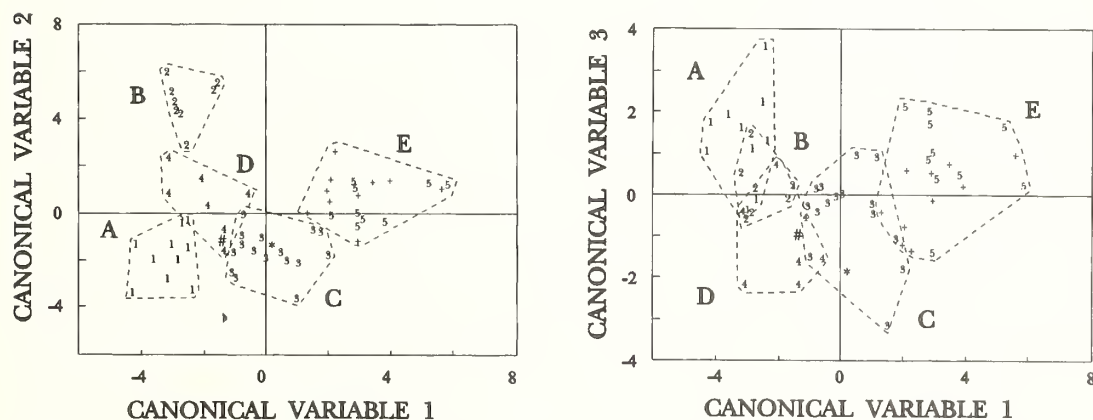
Statistical analyses

In order to recognize morphometric species, we used two major types of multivariate statistical procedures: (1) average linkage cluster analysis (UPGMA) and (2) canonical discriminant analysis. First, we analysed the measurement and count data for well-preserved colonies from each of the two stratigraphical levels and distinguished morphological clusters within each level. Then we compared less well-preserved colonies with the resulting morphological clusters. Finally we compared clusters between stratigraphical levels to recognize morphometric species. Our protocol is described in detail by Budd and Coates (1992) and Budd *et al.* (1994); the analyses were performed using the SAS version 6.09 for UNIX statistical procedures.

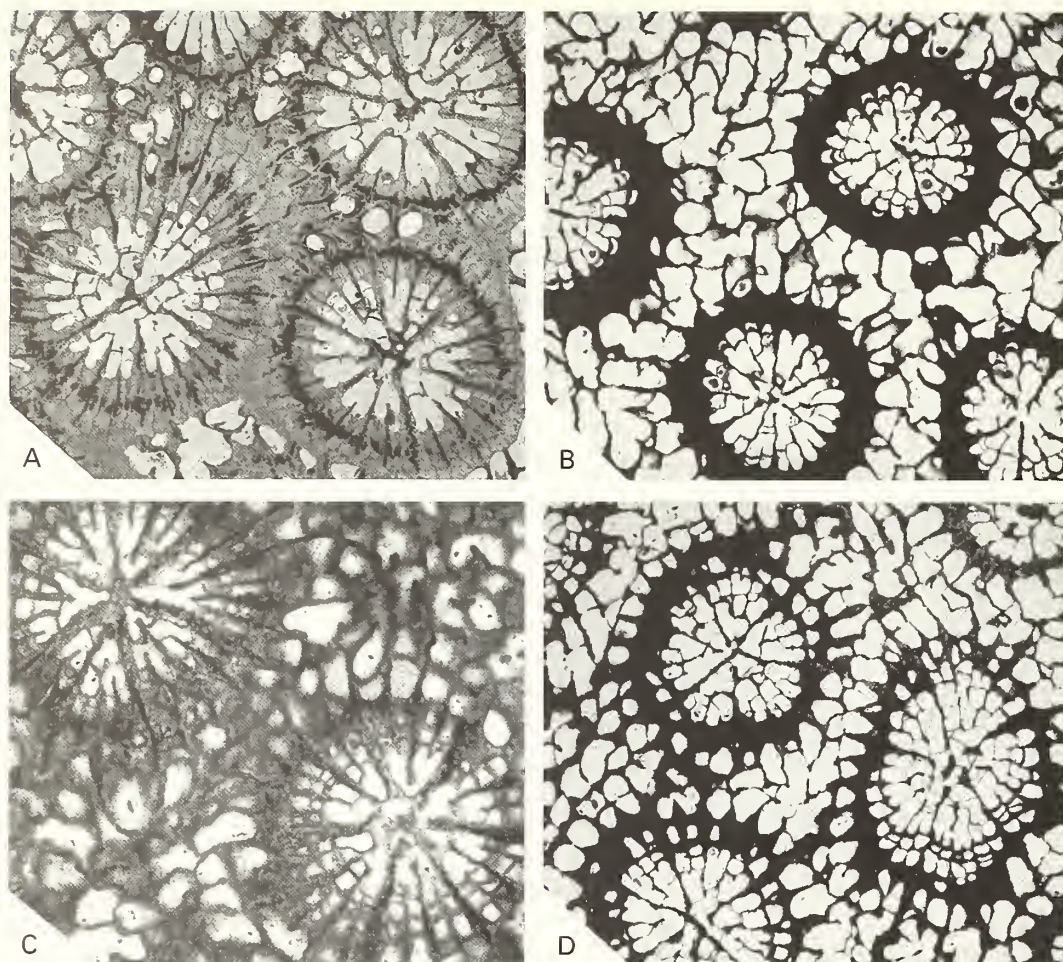
The first step involved performing average linkage cluster analysis on colonies from each of the two stratigraphical levels. In this initial cluster analysis, in order to prevent unknowingly assigning excessive weight to any one aspect of morphology, we selected a set of well-preserved, geometrically independent characters, with low Pearson's correlation coefficients (i.e. significantly less than 0.60). In the Upper Oligocene to Lower Miocene level, the characters consisted of NS, CD-MIN, NND, CL2, T1, T2. In the Middle to Upper Miocene level, the characters consisted of these six characters plus primary septum thickness (ST1). In the upper stratigraphical level, two ratios were also included: (1) the ratio between CD-MIN and CD-MAX ('CD-RAT') and (2) the ratio between ST2 and ST1 ('ST-RAT'). The first ratio served as an estimate of corallite ellipticity; the second served as an estimate of equality of the primary and secondary septa. Because the selected characters were found to have little or no correlation with corallite size (CD-MIN), no further transformations were made.

TABLE 3. Correlations between characters (Text-fig. 3) and canonical variables (CV) in three final canonical discriminant analyses. Logarithms were taken in characters derived from linear measurements. *Heavily weighted characters.

Character	CV1	CV2	CV3
1. Late Oligocene to Early Miocene (well preserved colonies only)			
NS	0.903*	-0.162	-0.015
CD-MIN	0.379	-0.345	-0.261
CD-RAT	-0.297	0.253	0.363
NND	-0.246	0.579*	-0.227
T1	0.324	0.562*	0.379
T2	-0.507	-0.017	0.491*
CLW	-0.036	-0.365	0.465*
Percentage variance explained	52.3	37.7	5.54
2. Mid to Late Miocene			
NS	-0.117	-0.141	0.316
CD-MIN	-0.672*	0.520	-0.179
CD-RAT	0.280	0.315	-0.178
NND	-0.426	0.650*	0.531
T1	0.326	0.725*	0.514
T2	0.267	-0.032	0.804*
CLW	-0.044	-0.084	-0.330
Percentage variance explained	45.4	38.7	15.9
3. Late Oligocene to Early Miocene (SP, SR unclassified)			
NS	0.900*	0.343	0.250
CD-MIN	0.513	-0.044	0.469*
NND	-0.464	0.527*	0.489*
T2	-0.438	-0.257	0.544*
Percentage variance explained	63.8	31.1	3.3

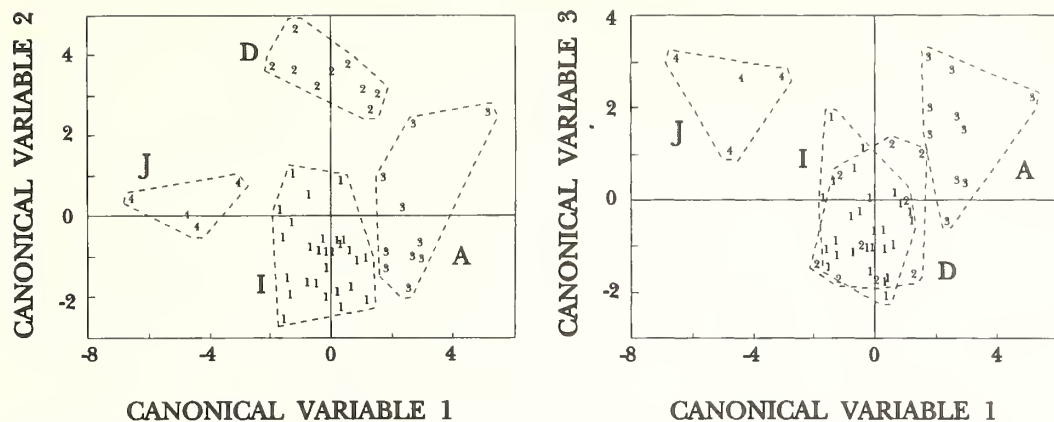


TEXT-FIG. 4. Plots of scores on the first three canonical variables in the canonical discriminant analysis of well-preserved Upper Oligocene to Lower Miocene colonies. Each point represents a colony mean. Symbols for each point refer to the cluster to which the colony was assigned. Dashed lines outline the range of variation within each cluster. Letters refer to morphometric species to which these clusters were later assigned. *, holotype of *T. carryensis* (MNHN, I.P.-R10521); #, holotype of *T. aquitaniensis* (MNHN, I.P.-R10518); +, topotypes of *T. ellisiana* (MNHN, I.P.).



TEXT-FIG. 5. Transverse thin sections of four of the five statistically recognized species in the Upper Oligocene to Lower Miocene. A, cluster 1 (morphometric species A), SUI-84718-A; B, cluster 2 (morphometric species B), SUI-51257-D; C, cluster 3 (morphometric species C), SUI-84765-C; D, cluster 5 (morphometric species E), MNHN, I.P., AFB# 135-C. All $\times 11$.

Because ecophenotypic plasticity is high in colonial scleractinians and corallites within colonies are highly variable (see Budd *et al.* 1994 for discussion), we used Mahalanobis distances when performing cluster analyses, in order to reduce variational noise and to emphasize differences *among* colonies rather than *within* colonies, when recognizing species quantitatively. To establish a cut-off for cluster recognition on the cluster analysis dendrograms, we arbitrarily subdivided the corallites for each colony into two groups of 'colony halves' in colonies, and calculated Mahalanobis distances among all halves within each stratigraphical level. Only colonies with more than five measured corallites were subdivided. Cut-offs for cluster recognition were established where: (1) the highest number of clusters could be recognized, and (2) more than 85 per cent. of the two halves of each colony belonged to the same cluster. In the Upper Oligocene to Lower Miocene level, a total of 60 halved and four unhalved colonies (localities = NE, EG, DX, LP) were included in the initial analysis, and eight clusters were recognized using a cut-off, in which the halves of only three of the



TEXT-FIG. 6. Plots of scores on the first three canonical variables in the canonical discriminant analysis of well-preserved Middle to Upper Miocene colonies. Each point represents a colony mean. Symbols for each point refer to the cluster to which the colony was assigned. Dashed lines outline the range of variation within each cluster. Letters refer to morphometric species to which the clusters were later assigned.

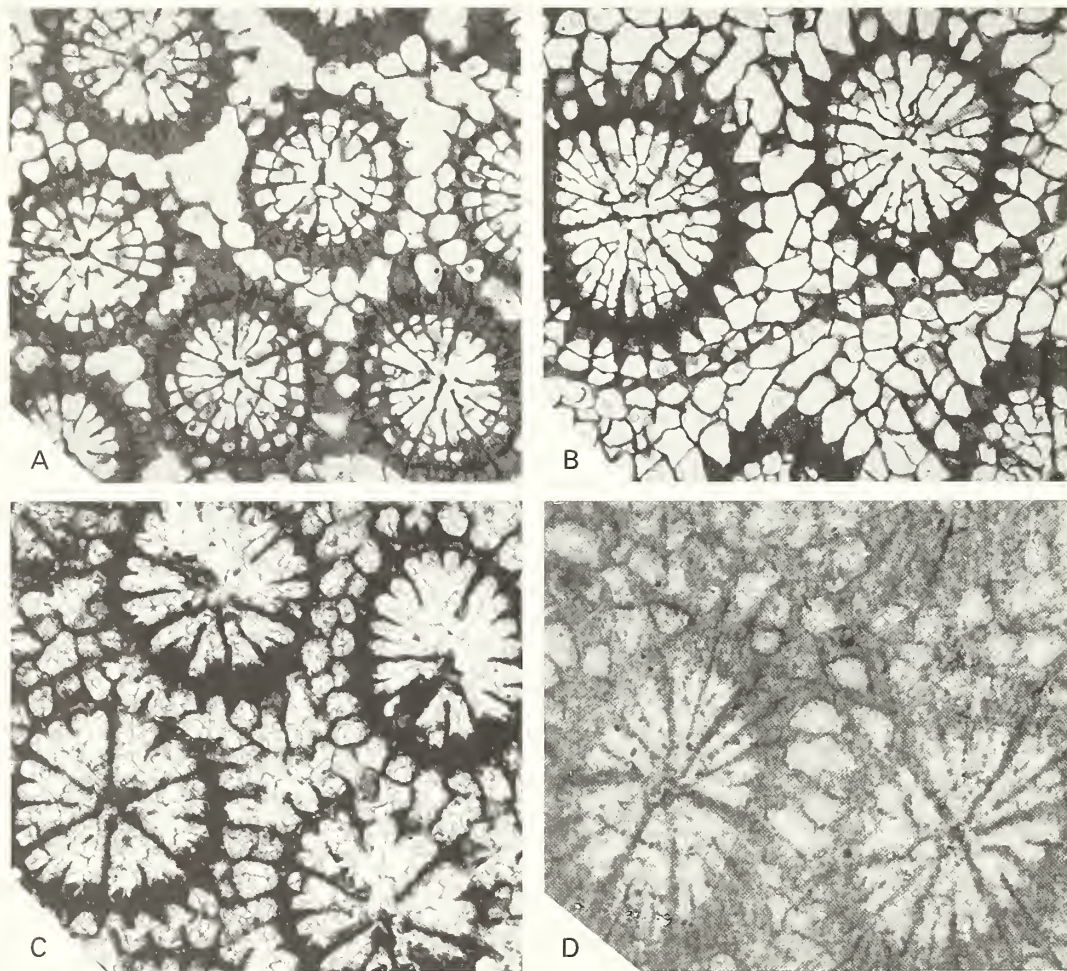
60 colonies (SUI 84735, 84764; MNHN, I.P.-AFB# 132) belonged to different clusters. In the Middle to Upper Miocene level, a total of 46 halved and five unhalved colonies (localities = TO, GR, BL, LD, SI, AL, MA) were included in the initial analysis, and seven clusters were recognized based on a cut-off in which the halves of only six of the 46 colonies (SUI 84704, 84652, 84658; IPUM 24884; MNHN, I.P.-AFB# 043, 179) belonged to different clusters.

Differences among the recognized clusters within each level were then examined using canonical discriminant analysis on data for each corallite. Logarithmic transformations were used for measurement data when performing these analyses, because sample sizes in different clusters were not equal and because measurement data in some clusters were skewed toward larger values. In the analyses, unhalved colonies and colonies whose halves belonged to different clusters were left unclassified. In the Upper Oligocene to Lower Miocene level, study of Mahalanobis distances among clusters and canonical discriminant plots suggested that three of the eight clusters were not significantly different from the other clusters. They were therefore combined, yielding a total of five clusters. In the Middle to Upper Miocene level, three of the seven clusters were not significantly different from the other clusters, and were therefore combined, yielding a total of four clusters.

Posterior probabilities were then used to assign unassigned colonies to one of the clusters in both data sets, and a series of iterative discriminant analyses was run using colony means. In the series, misclassified colonies were reassigned to different clusters until the highest percentage of colonies was classified correctly. In the Upper Oligocene to Lower Miocene level, 96.9 per cent. of the 64 colonies were classified correctly. In the Middle to Upper Miocene level, 100 per cent. of the 51 colonies were classified correctly.

The results of the final canonical discriminant analyses for the two levels are shown in Text-figures 4–7, and correlations between the original characters (Text-fig. 3) and the canonical variables are given in Table 3. In the Upper Oligocene to Lower Miocene (Text-fig. 4), number of septa per corallite (NS) was most strongly correlated with the first canonical variable (Table 3) which distinguished clusters 1, 2 and 4 from cluster 3 and, to a lesser degree, cluster 3 from cluster 5. Characters related to distance between corallites (NND, T1) were most strongly correlated with canonical variable 2 (Table 3) which distinguished cluster 1 from cluster 2, and cluster 3 from cluster 5. These differences among clusters in number of septa and distance between corallites were clearly seen in thin sections (Text-fig. 5). Furthermore, theca thickness (T2) and size of corallite centre (CLW) were correlated most strongly with canonical variable 3 (Table 3) which distinguished cluster 1 from cluster 4.

In the Middle to Upper Miocene (Text-fig. 6), corallite diameter (CD-MIN) was correlated most strongly with the first canonical variable (Table 3), which distinguished cluster 4 from clusters 1 and 2, and clusters 1 and 2 from cluster 3. Characters related to distance between corallites (NND, T1) were correlated most strongly with canonical variable 2 (Table 3) which distinguished cluster 2 from cluster 1. The differences among clusters in corallite diameter and distance between corallites are clearly seen in thin sections (Text-fig. 7). Furthermore, theca thickness (T2) was correlated most

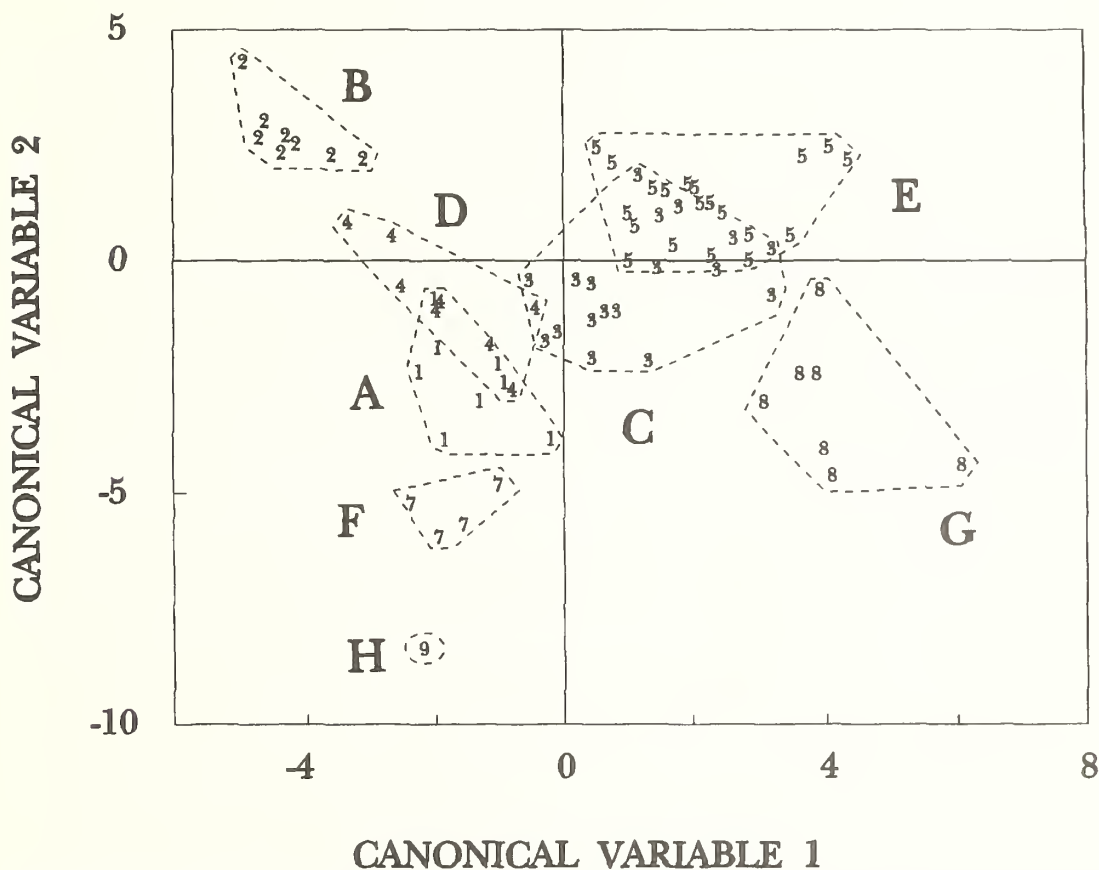


TEXT-FIG. 7. Transverse thin sections of the four statistically recognized species in the Middle to Upper Miocene. A, cluster 3 (morphometric species A), SUI-84673-H; B, cluster 2 (morphometric species D), SUI-84671-G; C, cluster 1 (morphometric species I), SUI-84703-E; D, cluster 4 (morphometric species J), SUI-84659-A. All $\times 11$.

strongly with canonical variable 3 (Table 3) which distinguished clusters 1 and 2 from clusters 3 and 4.

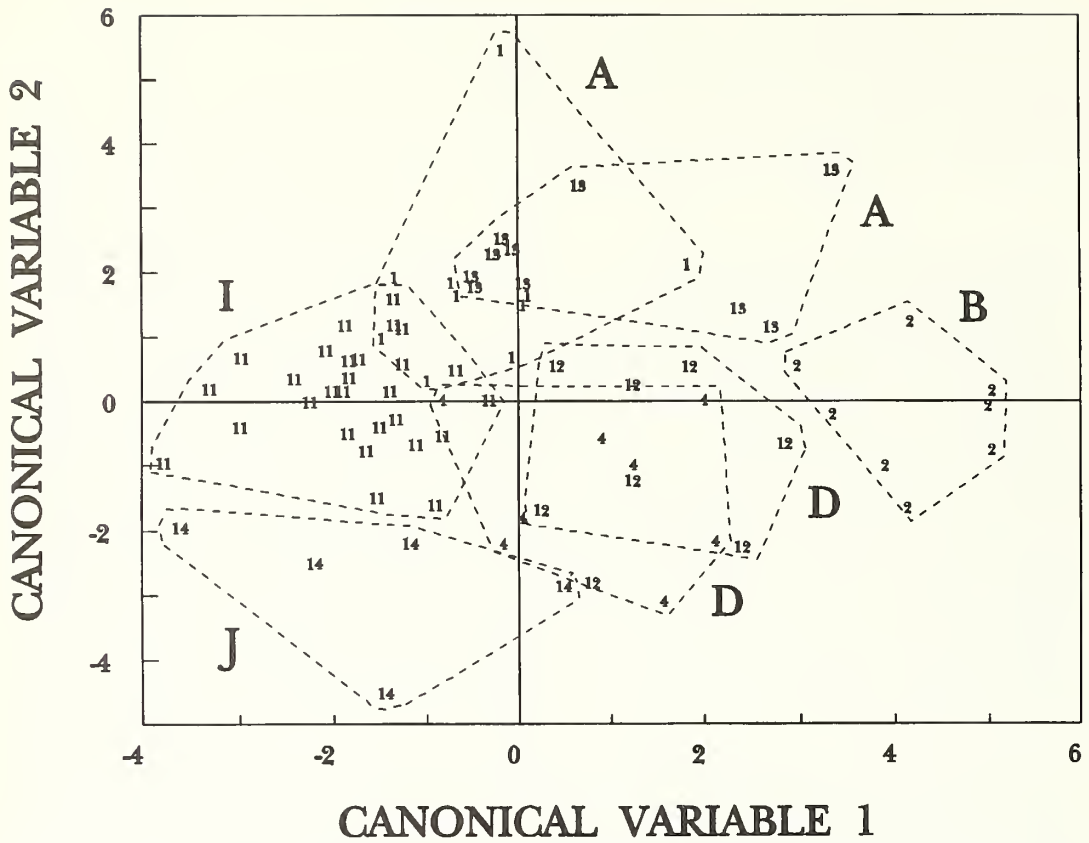
The next step in our protocol for recognizing morphometric species involved comparing statistically the canonical discriminant results above, with data from less well preserved colonies

collected at SP and SR. Measurements and counts on these colonies, similar to those in the analyses above, could only be made for four characters (Text-fig. 3): CD-MIN, NND, T2, NS. It is important to note, however, that these four characters were found to be the most important in distinguishing clusters in the analyses above. To make the statistical comparisons, a series of canonical discriminant analyses was run with data for the 64 Upper Oligocene to Lower Miocene colonies above, eight colonies from SP, and four colonies from SR. This analysis was run using four characters (CD-MIN, NND, T2, NS) and five groups (the five Upper Oligocene to Lower Miocene clusters in Text-fig. 4). The 12 newly added colonies were left unclassified. The results (Text-fig. 8)



TEXT-FIG. 8. Plot of scores on the first two canonical variables in the canonical discriminant analysis of Upper Oligocene to Lower Miocene colonies including SP and SR. Each point represents a colony mean. Symbols for each point refer to the cluster to which the colony was assigned. Dashed lines outline the range of variation within each cluster. Letters refer to morphometric species to which these clusters were later assigned.

showed that the 12 newly added colonies did not lie within the margins of any of the five Upper Oligocene to Lower Miocene clusters recognized earlier. Instead, seven of the colonies from SP formed a separate group with high values on CV1, which was correlated most strongly with number of septa per corallite (NS) (Table 3). Similarly, the four colonies from SR formed a group with low values on CV2, which was correlated most strongly with distance between corallites (NND) (Table 3). A single colony from SP had exceedingly low values on CV2 and CV3, which were correlated most strongly with distance between corallites (NND) and size (CD-MIN) respectively (Table 3).



TEXT-FIG. 9. Plot of scores on the first two canonical variables in the canonical discriminant analysis of three Upper Oligocene to Lower Miocene clusters and four Middle to Upper Miocene clusters. Each point represents a colony mean. Symbols for each point refer to the cluster to which the colony was assigned. Dashed lines outline the range of variation within each cluster. Letters refer to morphometric species to which these clusters were later assigned.

We therefore interpret the two groups and the one odd colony to represent three distinct clusters, yielding a total of eight clusters in the Upper Oligocene to Lower Miocene.

In the final step of our protocol for recognizing species, we compared the eight clusters in the Upper Oligocene to Lower Miocene with the four clusters in the Middle to Upper Miocene level using another series of canonical discriminant analyses. An initial analysis showed that no overlap occurred between Upper Oligocene to Lower Miocene clusters 3 and 5–8, and the four Middle to Upper Miocene clusters. Therefore, a separate analysis was run with only Upper Oligocene to Lower Miocene clusters 1, 2 and 4 and the four Middle to Upper Miocene clusters. A total of 78 colonies and seven characters (NS, CD-MIN, CD-RAT, NND, T1, T2, CL2) was used in the analysis. The results showed that differences between cluster 1 in level 1 and cluster 3 in level 2 are insignificant, and differences between cluster 4 in level 1 and cluster 2 in level 2 are insignificant (Text-fig. 9). These clusters were therefore linked.

The results of the final statistical analyses suggest that a total of 10 morphometric species of *Tarbellastraea* lived in the investigated basins during the Late Oligocene to Late Miocene. For the remainder of our discussion, these statistically recognized morphometric species will be referred to as 'A' to 'J'. The relationships between the ten morphometric species and the statistically

recognized clusters are: morphometric species A = cluster 1 in level 1 and cluster 3 in level 2; morphometric species B = cluster 2 in level 1; morphometric species C = cluster 3 in level 1; morphometric species D = cluster 4 in level 1 and cluster 2 in level 2; morphometric species E = cluster 5 in level 1; morphometric species F = cluster 6 in level 1; morphometric species G = cluster 7 in level 1; morphometric species H = cluster 8 in level 1; morphometric species I = cluster 1 in level 2; morphometric species J = cluster 4 in level 2. Means and standard deviations for the 12 measured characters (Text-fig. 3), NS, CD-RAT, and ST-RAT in the ten statistically recognized morphometric species are given in Appendix 1.

COMPARISON WITH TYPE SPECIMENS

Selection of type specimens

In order to assign names to the statistically recognized morphometric species, information was assembled about the primary types of all species and varieties that have previously been assigned to the genus *Tarbellastraea*. Primary types of species of the other seven genera in Table 1 were also considered, if they were collected in the regions that we considered in our study and if they strongly resembled *Tarbellastraea*. The final list of species is given in Table 4.

The calical surfaces of the type specimens of all species and varieties in Table 4 were first examined to determine if they possessed the diagnostic characteristics of *Tarbellastraea* given in Table 1. Two type specimens in Table 4 (*Leptastraea anomala* and *Orbicella eggenburgensis*) had a spongy columella (Text-fig. 10) and therefore clearly did not belong to *Tarbellastraea*. Another (*T. bliosi*) had paliform lobes, and therefore also did not belong. Three others (*Astrea astroites* = *T. organalis* Barta-Calmus, 1973, *Phyllocoenia ovalis* and *T. ukrainica*) had very large calices (> 5 mm) and four or more cycles of septa, and thus also did not belong. The remaining 25 species in Table 4 possessed the diagnostic characteristics of *Tarbellastraea*, and were therefore considered when determining names for the statistically recognized species.

Synonymies

Where possible, three measurements (NS, CD-MIN, NND) were made on calical surfaces of the types of the 25 species and varieties (Appendix 2). In two cases (*P. carryana* and *T. aquitaniensis*), thin sections were available of the holotype, so measurements were made directly from these and included in the original canonical discriminant analysis (Text-fig. 4). In one case (*Explanaria crassa*), the preservation was extremely poor, so no measurements could be made. In four other cases (*T. distans*, *A. ellisiana*, *T. edwardsi*, *T. ellisiana* var. *manthelanensis*), the type specimens were either lost or unavailable for measurement. For *T. distans*, measurements of the holotype were taken from Barta-Calmus (1973). For *T. edwardsi* and *T. ellisiana* var. *manthelanensis*, no measurements of the holotype exist in the literature; therefore, only a qualitative assessment could be made (see species descriptions of *T. profundata* and *T. bragai* below). For *A. ellisiana*, the holotype is lost, and the neotype designated by Alloiteau (1957, pl. 8, figs 4, 15; MNHN, I. P. R10933) could not be located. Therefore, measurements were made directly on thin sections of ten 'topotype' specimens in the general collections in Paris (MNHN, I. P., AFB# 129, 131, 133–140) labelled as '*Tarbellastraea ellisiana* (Defrance, 1826)' from Mérignac, Gironde (Aquitaine, France), and included in the original canonical discriminant analysis (Text-fig. 4). These specimens were amongst the material studied by Alloiteau (1957) in designating his neotype, and were also studied by Chevalier (1962). We hesitate to designate another neotype for *T. ellisiana*, as long as the potential exists for Alloiteau's (1957) neotype to be found.

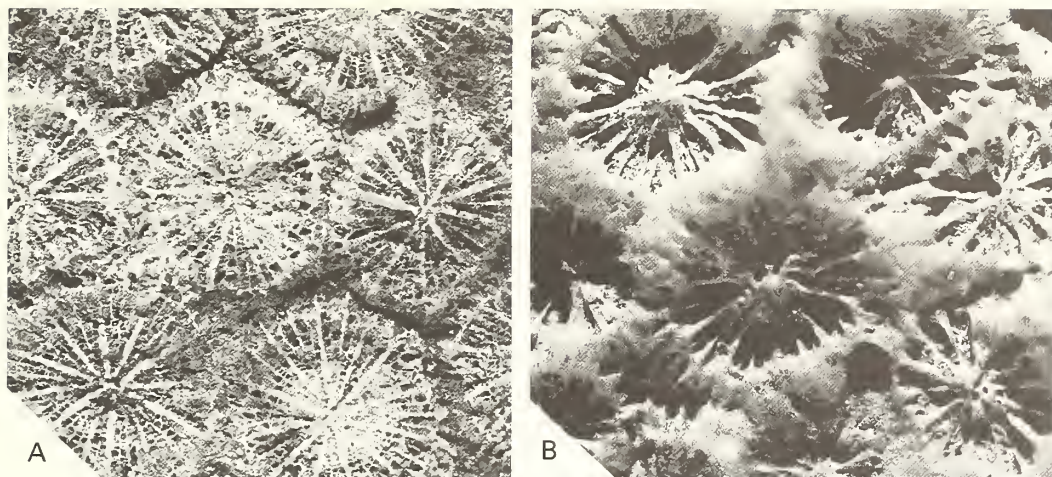
In the remaining 18 types, the three measurements (NS, CD-MIN, NND) were made on the calical surfaces of holotypes. As with the 13 localities (Table 2), one of us (FRB) determined the geological age dates for the type locality of each of the 25 species and varieties of *Tarbellastraea* by consulting with specialists on the local geology of the area, and by conducting a thorough review of the most recent literature (Table 5). As mentioned earlier, problems in age determination are to be discussed in fuller detail in a second paper.

TABLE 4. List of type specimens examined. Types of underlined species were found not to belong to *Tarbellastraea*. Measurements were made on types of species with code numbers. *, holotype lost; **, holotype not seen; ***, holotype not seen, but recent photograph examined.

Species	Code	Reference	Repository and catalogue number
<i>Tarbellastraea abditaxis</i> Chevalier, 1962	1	p. 204, pl. 6, fig. 10; pl. 23, fig. 8	MNHN, I.P.-R10525
<i>Leptastraea anomala</i> Michelotti, 1871	—	p. 306, pl. 8, fig. 7	MPUR-3302
<i>Tarbellastraea aquitaniensis</i> Chevalier, 1962	2	p. 201, pl. 9, fig. 12; pl. 23, fig. 2	MNHN, I.P.-R10518
<i>Tarbellastraea aquitaniensis</i> var. <i>termofurax</i> Chevalier, 1962	3	p. 202, pl. 8, figs 17–18	MNHN, I.P.-R10575
<i>Astrea astroites</i> Catullo, 1856	—	p. 59, pl. 12, fig. 4	MPUP-8261
<i>Tarbellastraea bliosi</i> Barta-Calmus, 1973	—	p. 280, pl. 15, figs 6–8	MNHN, I.P.-R55164
<i>Phyllocoenia carryana</i> d'Orbigny, 1852	4	p. 147	MNHN, I.P.-R10521
<i>Tarbellastraea carryensis</i> var. <i>major</i> Chevalier, 1962	5	p. 198, pl. 7, fig. 8	MNHN, I.P.-R10523
<i>Tarbellastraea carryensis</i> var. <i>minor</i> Chevalier, 1962	6	p. 198, pl. 10, figs 3, 9–10	MNHN, I.P.-R10522
<i>Heliastraea conoidea</i> Reuss, 1872	7	p. 240, pl. 10, fig. 3	NHFW-1854.XXXV.500
<i>Explanaria crassa</i> Reuss, 1847	—	p. 18, pl. 3, fig. 1	NHFW-1832.I.1358
*** <i>Tarbellastraea distans</i> Chevalier, 1962	8	p. 208, pl. 5, fig. 9	MNHN, I.P.-R55165
*** <i>Tarbellastraea edwardsi</i> Chevalier, 1955	—	p. 390, pl. 3, fig. 4	MNHN, I.P.-M00787 (= <i>P. archiaci</i>)
<i>Orbicella eggenburgensis</i> Kühn, 1925	—	p. 5, pl. 1, figs 1–2	KME
<i>Tarbellastraea</i> cf. <i>eggenburgensis</i> (Kühn); Chevalier, 1962	9	p. 202, pl. 6, fig. 3; pl. 24, fig. 9	MNHN, I.P.
<i>Orbicella eggenburgensis</i> var. <i>formosa</i> Kühn, 1925	10	p. 7, pl. 1, fig. 3	KME
<i>Tarbellastraea eggenburgensis</i> var. <i>andalusensis</i> Chevalier, 1962	11	p. 203, pl. 9, fig. 13; pl. 23, fig. 9	MNHN, I.P.-R10528
* <i>Astrea ellisiana</i> Defrance, 1826	—	p. 382	—
** <i>Tarbellastraea ellisiana</i> var. <i>manthelaniensis</i> Chevalier, 1962	—	p. 195, pl. 5, fig. 4	MNHN, I.P.-R10509
<i>Solenastraea manipulator</i> Reuss, 1872	12	p. 243, pl. 8, fig. 2	NHFW-1984/61
<i>Tarbellastraea mimbastensis</i> Chevalier, 1962	13	p. 199, pl. 5, fig. 3; pl. 23, fig. 1	MNHN, I.P.-R10529
*** <i>Phyllocoenia ovalis</i> Gümbel, 1861	—	p. 666	BSPHGM-AS-38
<i>Astraea prevostiana</i> Milne Edwards and Haime, 1850	14	p. 110	MNHN, I.P.-M01184
<i>Astrea profundata</i> Catullo, 1856	15	p. 56, pl. 11, fig. 6	MPUP-8142
<i>Astraea ranlini</i> Milne Edwards and Haime, 1850	16	p. 110	MNHN, I.P.-M01281
<i>Astraea reussiana</i> Milne-Edwards and Haime, 1850	17	p. 110	NHFW-1846.37.967 (= <i>E. astroites</i>)
<i>Tarbellastraea reussiana</i> var. <i>echinulata</i> Chevalier, 1962	18	p. 206, pl. 5, fig. 18; pl. 24, fig. 7	MNHN, I.P.-R10510
<i>Tarbellastraea siciliae</i> Chevalier, 1962	19	p. 207, pl. 7, fig. 10; pl. 23, fig. 7	MNHN, I.P.-R10527
<i>Explanaria tenera</i> Reuss, 1847	20	p. 18, pl. 3, fig. 2	NHFW-1872.XIII.61
<i>Orbicella transylvanica</i> Kühn, 1925	21	p. 4	NHFW-1872.XIII.56
** <i>Tarbellastraea ukrainica</i> Kuzmicheva, 1987	—	p. 105, pl. 16, figs 1–2	MGU-N185/507

TABLE 4. List of type specimens examined. Types of underlined species were found not to be belong to *Tarbellastraea*. Measurements were made on types of species with code numbers. *, holotype lost; **, holotype not seen; ***, holotype not seen, but recent photograph examined.

Species	Code	Reference	Repository and catalogue number
<i>Tarbellastraea abdita</i> Chevalier, 1962	1	p. 204, pl. 6, fig. 10; pl. 23, fig. 8	MNHN, I.P.-R10525
<i>Leptastraea anomala</i> Michelotti, 1871	—	p. 306, pl. 8, fig. 7	MPUR-3302
<i>Tarbellastraea aquitaniensis</i> Chevalier, 1962	2	p. 201, pl. 9, fig. 12; pl. 23, fig. 2	MNHN, I.P.-R10518
<i>Tarbellastraea aquitaniensis</i> var. <i>termofurae</i> Chevalier, 1962	3	p. 202, pl. 8, figs 17-18	MNHN, I.P.-R10575
<i>Astrea astroites</i> Catullo, 1856	—	p. 59, pl. 12, fig. 4	MPUP-8261
<i>Tarbellastraea bliosi</i> Barta-Calmus, 1973	—	p. 280, pl. 15, figs 6-8	MNHN, I.P.-R55164
<i>Phyllocoenia carryana</i> d'Orbigny, 1852	4	p. 147	MNHN, I.P.-R10521
<i>Tarbellastraea carryensis</i> var. <i>major</i> Chevalier, 1962	5	p. 198, pl. 7, fig. 8	MNHN, I.P.-R10523
<i>Tarbellastraea carryensis</i> var. <i>minor</i> Chevalier, 1962	6	p. 198, pl. 10, figs 3, 9-10	MNHN, I.P.-R10522
<i>Heliastraea conoidea</i> Reuss, 1872	7	p. 240, pl. 10, fig. 3	NHMW-1854.XXXV.500
<i>Explanaria crassa</i> Reuss, 1847	—	p. 18, pl. 3, fig. 1	NHMW-1832.I.1358
*** <i>Tarbellastraea distans</i> Chevalier, 1962	8	p. 208, pl. 5, fig. 9	MNHN, I.P.-R55165
*** <i>Tarbellastraea edwardsi</i> Chevalier, 1955	—	p. 390, pl. 3, fig. 4	MNHN, I.P.-M00787 (= <i>P. archiaci</i>)
<i>Orbicella eggenburgensis</i> Kühn, 1925	—	p. 5, pl. 1, figs 1-2	KME
<i>Tarbellastraea</i> cf. <i>eggenburgensis</i> (Kühn); Chevalier, 1962	9	p. 202, pl. 6, fig. 3; pl. 24, fig. 9	MNHN, I.P.
<i>Orbicella eggenburgensis</i> var. <i>formosa</i> Kühn, 1925	10	p. 7, pl. 1, fig. 3	KME
<i>Tarbellastraea eggenburgensis</i> var. <i>andalousiensis</i> Chevalier, 1962	11	p. 203, pl. 9, fig. 13; pl. 23, fig. 9	MNHN, I.P.-R10528
* <i>Astrea ellisiana</i> Defrance, 1826	—	p. 382	—
** <i>Tarbellastraea ellisiana</i> var. <i>manthelamensis</i> Chevalier, 1962	—	p. 195, pl. 5, fig. 4	MNHN, I.P.-R10509
<i>Solenastraea manipulata</i> Reuss, 1872	12	p. 243, pl. 8, fig. 2	NHMW-1984/61
<i>Tarbellastraea minbasiensis</i> Chevalier, 1962	13	p. 199, pl. 5, fig. 3; pl. 23, fig. 1	MNHN, I.P.-R10529
*** <i>Phyllocoenia ovalis</i> Gümbel, 1861	—	p. 666	BSPHGM-AS-38
<i>Astrea prevostiana</i> Milne Edwards and Haime, 1850	14	p. 110	MNHN, I.P.-M01184
<i>Astrea profundata</i> Catullo, 1856	15	p. 56, pl. 11, fig. 6	MPUP-8142
<i>Astrea raulini</i> Milne Edwards and Haime, 1850	16	p. 110	MNHN, I.P.-M01281
<i>Astrea reussiana</i> Milne-Edwards and Haime, 1850	17	p. 110	NHMW-1846.37.967 (= <i>E. astroites</i>)
<i>Tarbellastraea reussiana</i> var. <i>echinulata</i> Chevalier, 1962	18	p. 206, pl. 5, fig. 18; pl. 24, fig. 7	MNHN, I.P.-R10510
<i>Tarbellastraea siciliæ</i> Chevalier, 1962	19	p. 207, pl. 7, fig. 10; pl. 23, fig. 7	MNHN, I.P.-R10527
<i>Explanaria tenera</i> Reuss, 1847	20	p. 18, pl. 3, fig. 2	NHMW-1872.XIII.61
<i>Orbicella transsylvanica</i> Kühn, 1925	21	p. 4	NHMW-1872.XIII.56
** <i>Tarbellastraea ukrainica</i> Kuzmicheva, 1987	—	p. 105, pl. 16, figs 1-2	MGU-N185/507



TEXT-FIG. 10. Calical surfaces of holotypes of two species that have been previously assigned to *Tarbellastraea* but do not belong in this genus. A, *Astrea astroites* Catullo, 1856 (= *Tarbellastraea organalis* Barta-Calmus, 1973); MPUP-8261. B, *Leptastraea anomala* Michelotti, 1871; MPUR-3302. Both $\times 5$.

In the three cases where thin section measurements were made (*T. aquitaniensis*, *P. carryana*, *A. ellisiana*), the type specimens for these species were assigned to the statistically recognized species as part of the canonical discriminant analyses, and synonymies between the statistical species and these type specimens were determined on the basis of the results of this analysis (Text-fig. 4). In this procedure, *T. aquitaniensis* was only synonymized questionably with statistical species D, because of the large distance of its holotype from the centre of that cluster. The type specimen for *P. carryana* clearly lay in the centre of statistical species C, and the topotypes for *A. ellisiana* definitely belonged to statistical species E. Therefore, synonymies for these two species were made without question.

In the remaining 19 cases (including *T. distans*) where measurements were made on calical surfaces of holotypes (Appendix 2), bivariate plots were constructed for number of septa (NS) vs distance between corallites (NND), and for corallite diameter (CD) vs distance between corallites (NND) using the same two major stratigraphical levels as in the canonical discriminant analyses: (1) Upper Oligocene to Lower Miocene and (2) Middle to Upper Miocene (Text-fig. 11). On each plot, type specimens (labelled 1–21) were considered to be synonymous with a given statistically recognized morphometric species (labelled A–J), if they lay near the statistical species on both of the two plots. In two cases (type 13 with morphometric species E in the Upper Oligocene to Lower Miocene; type 21 with morphometric species I in the Middle to Upper Miocene), only questionable synonymies were made because of the large distance between the type specimen and the statistical species. A questionable synonymy was also made for type 6 with morphometric species F, because of difference in structure of the columella and wall. Two groups of types (1, 3, 9, 11 in the Upper Oligocene to Lower Miocene; 5, 15 in the Middle to Upper Miocene) formed clusters separate from any of the statistical species, and therefore were considered to be distinct morphometric species unrepresented in the statistical analyses. A summary of the results of these comparisons is given in Table 6.

In general, a total of 12 species of *Tarbellastraea* was found to have lived in the investigated European and Mediterranean regions during the Late Oligocene to Late Miocene. The distinguishing characteristics for these 12 species are summarized in Table 7, and formal descriptions are provided in the section below on systematic palaeontology. Although the overall number of species is similar to that recognized by Chevalier (1962), nine of his 19 species and

TABLE 5. List of localities for type specimens of *Tarbellastraea* with current interpretations of their geological age.

Species	Type locality	Age	Age reference
1. <i>Tarbellastraea abdita</i>	Sciolze (Torino, Italy)	Burdigalian-Langhian	Bonsignore <i>et al.</i> 1969
2. <i>Tarbellastraea aquitaniensis</i>	Le Peloua (Gironde, France)	Early Burdigalian	Cahuzac and Chaix 1993
3. <i>Tarbellastraea aquitaniensis</i> var. <i>termofuriae</i>	Termô Fôrà (Torino, Italy)	Burdigalian-Langhian	Bonsignore <i>et al.</i> 1969
4. <i>Phyllocoenia carryana</i>	Carry-le-Rouet (Bouches-du-Rhône, France)	Late Chattian	Monleau <i>et al.</i> 1988
5. <i>Tarbellastraea carryensis</i> var. <i>major</i>	Carry-le-Rouet (Bouches-du-Rhône, France)	Late Chattian	Monleau <i>et al.</i> 1988
6. <i>Tarbellastraea carryensis</i> var. <i>minor</i>	Carry-le-Rouet (Bouches-du-Rhône, France)	Late Chattian	Monleau <i>et al.</i> 1988
7. <i>Heliastrea conoidea</i>	Enzesfeld (Vienna, Austria)	Badenian	Piller and Kleemann 1991
— <i>Explanaria crassa</i>	Vienna Basin (Austria)	Badenian	Piller and Kleemann 1991
8. <i>Tarbellastraea distans</i>	Albugnano (Torino, Italy)	Burdigalian-Langhian	Bonsignore <i>et al.</i> 1969
— <i>Tarbellastraea edwardsi</i>	Gaas (Landes, France)	Stampian	Chevalier 1955
9. <i>Tarbellastraea</i> cf. <i>eggenburgensis</i>	Sciolze, Albugnano (Torino, Italy)	Burdigalian-Langhian	Bonsignore <i>et al.</i> 1969
10. <i>Orbicella eggenburgensis</i> var. <i>formosa</i>	Eggenburg (Vienna, Austria)	Eggenburgian	Steininger and Senes 1971
11. <i>Tarbellastraea eggenburgensis</i> var. <i>andalousiensis</i>	Quentar (Granada, Spain)	Late Tortonian	Braga <i>et al.</i> 1990
— <i>Tarbellastraea ellisiana</i>	Mérignac (Gironde, France)	Early Burdigalian	Cahuzac and Chaix 1993
— <i>Tarbellastraea ellisiana</i> var. <i>manthelanensis</i>	Manthelan (Indre-et-Loire, France)	Langhian	Cavelier <i>et al.</i> 1980
12. <i>Solenastraea manipolata</i>	Enzesfeld (Vienna, Austria)	Badenian	Piller and Kleemann 1991
13. <i>Tarbellastraea mimbastensis</i>	Mimbaste (Landes, France)	Early Burdigalian	Cahuzac 1984
14. <i>Astraea prevostiana</i>	Malta	Late Tortonian-Early Messinian	Giannelli and Salvatorini 1975; Pedley 1989
15. <i>Astraea profundata</i>	Montecchio (Vicenza, Italy)	Rupelian	Bosellini 1988
16. <i>Astraea raulini</i>	Le Peloua (Gironde, France)	Early Burdigalian	Poignant and Pujol 1978
17. <i>Astraea reussiana</i>	Vienna Basin (Austria)	Badenian	Piller and Kleemann 1991
18. <i>Tarbellastraea reussiana</i> var. <i>echinulata</i>	Mérignac (Gironde, France)	Early Burdigalian	Cahuzac and Chaix 1993
19. <i>Tarbellastraea siciliæ</i>	Landro (Sicily, Italy)	Late Tortonian	Catalano 1979
20. <i>Explanaria tenera</i>	Vienna Basin (Austria)	Badenian	Piller and Kleemann 1991
21. <i>Orbicella transsylvanica</i>	Enzesfeld (Vienna, Austria)	Badenian	Piller and Kleemann 1991

TABLE 5. List of localities for type specimens of *Tarbellastraea* with current interpretations of their geological age.

Species	Type locality	Age	Age reference
1. <i>Tarbellastraea abditaxis</i>	Sciolze (Torino, Italy)	Burdigalian-Langhian	Bonsignore <i>et al.</i> 1969
2. <i>Tarbellastraea aquitaniensis</i>	Le Peloua (Gironde, France)	Early Burdigalian	Cahuzac and Chaix 1993
3. <i>Tarbellastraea aquitaniensis</i> var. <i>termofurac</i>	Termò Forà (Torino, Italy)	Burdigalian-Langhian	Bonsignore <i>et al.</i> 1969
4. <i>Phyllocoenia carryana</i>	Carry-le-Rouet (Bouches-du-Rhône, France)	Late Chattian	Monleau <i>et al.</i> 1988
5. <i>Tarbellastraea carryensis</i> var. <i>major</i>	Carry-le-Rouet (Bouches-du-Rhône, France)	Late Chattian	Monleau <i>et al.</i> 1988
6. <i>Tarbellastraea carryensis</i> var. <i>minor</i>	Carry-le-Rouet (Bouches-du-Rhône, France)	Late Chattian	Monleau <i>et al.</i> 1988
7. <i>Heliastraea conoidea</i>	Enzesfeld (Vienna, Austria)	Badenian	Piller and Kleemann 1991
— <i>Explanaria crassa</i>	Vienna Basin (Austria)	Badenian	Piller and Kleemann 1991
8. <i>Tarbellastraea distans</i>	Albugnano (Torino, Italy)	Burdigalian-Langhian	Bonsignore <i>et al.</i> 1969
— <i>Tarbellastraea edwardsi</i>	Gaas (Landes, France)	Stampian	Chevalier 1955
9. <i>Tarbellastraea</i> cf. <i>eggenburgensis</i>	Sciolze, Albugnano (Torino, Italy)	Burdigalian-Langhian	Bonsignore <i>et al.</i> 1969
10. <i>Orbicella eggenburgensis</i> var. <i>formosa</i>	Eggenburg (Vienna, Austria)	Eggenburgian	Steininger and Senes 1971
11. <i>Tarbellastraea eggenburgensis</i> var. <i>andalousiensis</i>	Quentar (Granada, Spain)	Late Tortonian	Braga <i>et al.</i> 1990
— <i>Tarbellastraea ellisiana</i>	Mérignac (Gironde, France)	Early Burdigalian	Cahuzac and Chaix 1993
— <i>Tarbellastraea ellisiana</i> var. <i>manthelanensis</i>	Manthelan (Indre-et-Loire, France)	Langhian	Cavelier <i>et al.</i> 1980
12. <i>Solenastraea manipulata</i>	Enzesfeld (Vienna, Austria)	Badenian	Piller and Kleemann 1991
13. <i>Tarbellastraea nimbastensis</i>	Mimbaste (Landes, France)	Early Burdigalian	Cahuzac 1984
14. <i>Astraea prevostiana</i>	Malta	Late Tortonian-Early Messinian	Giannelli and Salvatorini 1975; Pedley 1989
15. <i>Astraea profunda</i>	Montecchio (Vicenza, Italy)	Rupelian	Bosellini 1988
16. <i>Astraea raulini</i>	Le Peloua (Gironde, France)	Early Burdigalian	Poignant and Pujol 1978
17. <i>Astraea reussiana</i>	Vienna Basin (Austria)	Badenian	Piller and Kleemann 1991
18. <i>Tarbellastraea reussiana</i> var. <i>echimulata</i>	Mérignac (Gironde, France)	Early Burdigalian	Cahuzac and Chaix 1993
19. <i>Tarbellastraea sicilae</i>	Landro (Sicily, Italy)	Late Tortonian	Catalano 1979
20. <i>Explanaria tenera</i>	Vienna Basin (Austria)	Badenian	Piller and Kleemann 1991
21. <i>Orbicella transsylvanica</i>	Enzesfeld (Vienna, Austria)	Badenian	Piller and Kleemann 1991

TABLE 6. List of species found to be synonymous by examination of measurements made on type specimens, as shown in Text-figure 11.

Code	Species found to be synonymous	Name assigned
	Statistical species A	
20	<i>Explanaria tenera</i> Reuss, 1847	<i>Tarbellastraea tenera</i> (Reuss, 1847)
7	<i>Heliastraea conoidea</i> Reuss, 1872	
19	<i>Tarbellastraea siciliae</i> Chevalier, 1962	
	Statistical species B	
8	<i>Tarbellastraea distans</i> Chevalier, 1962	<i>Tarbellastraea distans</i> (Chevalier, 1962)
	Statistical species C	
4	<i>Phyllocoenia carryana</i> d'Orbigny, 1852	<i>Tarbellastraea carryensis</i> (d'Orbigny, 1852)
	Statistical species D	
16	<i>Astraea raulini</i> Milne Edwards and Haime, 1850	<i>Tarbellastraea raulini</i> (Milne Edwards and Haime, 1850)
14	<i>Astraea prevostiana</i> Milne Edwards and Haime, 1850	
2	? <i>Tarbellastraea aquitaniensis</i> Chevalier, 1962	
18	<i>Tarbellastraea reussiana</i> var. <i>echinulata</i> Chevalier, 1962	
	Statistical species E	
—	<i>Astraea ellisiana</i> Defrance, 1826	<i>Tarbellastraea ellisiana</i> (Defrance, 1826)
13	? <i>Tarbellastraea mimbastensis</i> Chevalier, 1962	
	Statistical species F	
6	? <i>Tarbellastraea carryensis</i> var. <i>minor</i> Chevalier, 1962	<i>Tarbellastraea chevalieri</i> sp. nov.
	Statistical species G	<i>Tarbellastraea russoi</i> sp. nov.
	Statistical species H	<i>Tarbellastraea salentinensis</i> sp. nov.
	Statistical species I	
17	<i>Astraea reussiana</i> Milne Edwards and Haime, 1850	<i>Tarbellastraea reussiana</i> (Milne Edwards and Haime, 1850)
12	<i>Solenastraea manipolata</i> Reuss, 1872	
21	? <i>Orbicella transsylvanica</i> Kühn, 1925	
	Statistical species J	
10	<i>Tarbellastraea eggenburgensis</i> var. <i>formosa</i> Kühn, 1925	<i>Tarbellastraea bragai</i> sp. nov. <i>Tarbellastraea abditaxis</i> (Chevalier, 1962)
1	<i>Tarbellastraea abditaxis</i> Chevalier, 1962	
3	<i>Tarbellastraea aquitaniensis</i> var. <i>termofuriae</i> Chevalier, 1962	
9	<i>Tarbellastraea</i> cf. <i>eggenburgensis</i> Chevalier, 1962	
11	<i>Tarbellastraea eggenburgensis</i> var. <i>andalousiensis</i> Chevalier, 1962	
15	<i>Astraea profundata</i> Catullo, 1856	<i>Tarbellastraea profundata</i> (Catullo, 1856)
5	<i>Tarbellastraea carryensis</i> var. <i>major</i> Chevalier, 1962	

varieties are synonymized, and two new species are recognized from the Oligocene of Italy. Thus, our results suggest that some of Chevalier's (1962) species and varieties can be synonymized, but certainly not all, as advocated by Best *et al.* (1984).

In general, early during the evolution of the genus (Late Oligocene to Early Miocene), species exhibited a wider range of morphologies (Text-fig. 11). Number of septa per corallite (NS) ranged from 18 to 38, and corallite diameter (CD-MIN) ranged from 1.7 mm to 3.5 mm. In contrast, during the Mid to Late Miocene, number of septa per corallite (NS) ranged from 24 to 26, and corallite diameter (CD-MIN) ranged from 1.4 mm to 2.5 mm. Therefore, *Tarbellastraea* exhibited a striking decrease in overall morphological disparity through geological time.

TABLE 7. Distinguishing morphological characteristics of 12 species of *Tarbellastraea* that were found to have lived in the investigated regions during the Late Oligocene to Late Miocene. *, 'corallite spacing' refers to the distance between centres of adjacent calices.

Species	Colony form	Corallite shape	Corallite size (mm)	Corallite spacing* (mm)	Septal number	1st septal cycle length (mm)	Costae length (mm)
<i>T. abditaxis</i>	Massive	Round	1.5-2.3	2.2-3.0	23-25	< 1.1	Moderately long
<i>T. bragai</i>	Laminar, columnar or branched	Irregular	1.8-2.3	3.4-4.7	23-25	0.87-1.11	0.39-0.53
<i>T. carryensis</i>	Massive-columnar	Irregular	2.1-2.9	3.1-4.1	26-33	0.86-1.16	0.42-0.62
<i>T. chevalieri</i>	Massive	Round-irregular	1.6-2.4	2.5-3.4	19-25	0.66-0.94	Relatively short
<i>T. distans</i>	Massive	Round	1.7-2.1	4.1-5.2	23-26	0.68-0.84	0.49-0.79
<i>T. ellisiana</i>	Massive	Irregular	1.9-2.5	2.9-3.9	27-35	0.69-1.01	0.47-0.77
<i>T. profunda</i>	Massive-digitate	Round	3.3-3.5	4.8-5.0	36-39	1.2-1.6	Moderately long
<i>T. raulini</i>	Massive	Regular	1.6-2.3	3.0-4.2	23-25	0.75-0.97	0.39-0.63
<i>T. reussiana</i>	Massive	Round-irregular	1.7-2.1	2.5-3.3	23-25	0.67-0.87	0.32-0.47
<i>T. russoi</i>	Massive, knobby	Round-irregular	2.3-3.3	2.7-4.1	30-37	0.88-1.24	Moderately long
<i>T. salentinensis</i>	Massive-digitate	Irregular	1.8-2.5	2.6-2.8	15-22	0.70-0.86	Relatively short
<i>T. tenera</i>	Columnar	Round	1.6-2.0	2.7-3.7	23-25	0.63-0.79	0.42-0.78

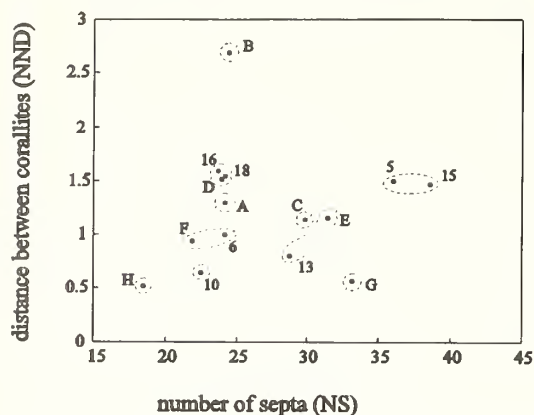
Species	Wall structure	Wall thickness (mm)	Columella development	Columella form	Columella thickness (mm)	Endothecal dissepiments	Exotheca
<i>T. abditaxis</i>	Septothecal	0.15-0.25	Strong or weak	?Tied to septa	< 0.08	Weak or absent	No distinct banding
<i>T. bragai</i>	Septothecal	0.09-0.19	Strong or weak	Tied to septa	0.05-0.13	Weak or absent	Dense, horizontal layering
<i>T. carryensis</i>	Septothecal or partially parathecal	0.02-0.16	Strong or weak	Tied to septa	< 0.14	Well-developed; 1-3 rings	No distinct banding
<i>T. chevalieri</i>	Septothecal	0.09-0.29	Weak or absent	Tied to septa	0.05-0.09	Weak or absent	No distinct banding
<i>T. distans</i>	Septothecal	0.05-0.21	Weak	Free or tied to septa	< 0.08	Well-developed; 1 ring	Strong density banding
<i>T. ellisiana</i>	Septothecal or partially parathecal	0.01-0.20	Strong	Tied to septa	0.1-0.2	Well-developed; 1-3 rings	Strong banding and dense coenosteum
<i>T. profundata</i>	Septothecal	< 0.1	Strong	Tied to septa	< 0.13	Well-developed; 1-2 rings	No distinct banding
<i>T. railini</i>	Septothecal	0.04-0.12	Weak	Tied to septa	0.05	Well-developed; 1-2 rings	Sparse density banding
<i>T. reussiana</i>	Septothecal	0.04-0.14	Weak	Free or tied to septa	0.08	Weak; 1 ring	No distinct banding
<i>T. russoi</i>	Septothecal	0.05-0.13	Strong	Tied to septa or free	< 0.15	Well-developed; 2 rings	Strong density banding
<i>T. salentinensis</i>	Septothecal	0.04-0.07	Weak or absent	Free or tied to septa	Not available	Absent	Dense horizontal layering
<i>T. tenera</i>	Septothecal	0.08-0.26	Strong	Tied to septa	0.06-0.15	Weak; 1 ring	Some density banding

TABLE 7. Distinguishing morphological characteristics of 12 species of *Tarballastraea* that were found to have lived in the investigated regions during the Late Oligocene to Late Miocene. *, 'corallite spacing' refers to the distance between centres of adjacent calices.

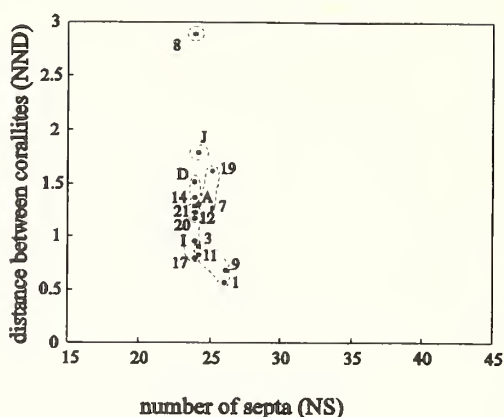
Species	Colony form	Corallite shape	Corallite size (mm)	Corallite spacing* (mm)	Septal number	1st septal cycle length (mm)	Costae length (mm)
<i>T. abditaxis</i>	Massive	Round	1.5–2.3	2.2–3.0	23–25	< 1.1	Moderately long
<i>T. bragai</i>	Laminar, columnar or branched	Irregular	1.8–2.3	3.4–4.7	23–25	0.87–1.11	0.39–0.53
<i>T. carryensis</i>	Massive–columnar	Irregular	2.1–2.9	3.1–4.1	26–33	0.86–1.16	0.42–0.62
<i>T. chevalieri</i>	Massive	Round–irregular	1.6–2.4	2.5–3.4	19–25	0.66–0.94	Relatively short
<i>T. distans</i>	Massive	Round	1.7–2.1	4.1–5.2	23–26	0.68–0.84	0.49–0.79
<i>T. ellisiaua</i>	Massive	Irregular	1.9–2.5	2.9–3.9	27–35	0.69–1.01	0.47–0.77
<i>T. profundata</i>	Massive–digitate	Round	3.3–3.5	4.8–5.0	36–39	1.2–1.6	Moderately long
<i>T. raulini</i>	Massive	Regular	1.6–2.3	3.0–4.2	23–25	0.75–0.97	0.39–0.63
<i>T. reussiana</i>	Massive	Round–irregular	1.7–2.1	2.5–3.3	23–25	0.67–0.87	0.32–0.47
<i>T. russoi</i>	Massive, knobby	Round–irregular	2.3–3.3	2.7–4.1	30–37	0.88–1.24	Moderately long
<i>T. salentinensis</i>	Massive–digitate	Irregular	1.8–2.5	2.6–2.8	15–22	0.70–0.86	Relatively short
<i>T. tenera</i>	Columnar	Round	1.6–2.0	2.7–3.7	23–25	0.63–0.79	0.42–0.78

Species	Wall structure	Wall thickness (mm)	Columella development	Columella form	Columella thickness (mm)	Endothecal dissepiments	Exotheca
<i>T. abditaxis</i>	Septothecal	0.15–0.25	Strong or weak	?Tied to septa	< 0.08	Weak or absent	No distinct banding
<i>T. bragai</i>	Septothecal	0.09–0.19	Strong or weak	Tied to septa	0.05–0.13	Weak or absent	Dense, horizontal layering
<i>T. carryensis</i>	Septothecal or partially parathecal	0.02–0.16	Strong or weak	Tied to septa	< 0.14	Well-developed; 1–3 rings	No distinct banding
<i>T. chevalieri</i>	Septothecal	0.09–0.29	Weak or absent	Tied to septa	0.05–0.09	Weak or absent	No distinct banding
<i>T. distans</i>	Septothecal	0.05–0.21	Weak	Free or tied to septa	< 0.08	Well-developed; 1 ring	Strong density banding
<i>T. ellisiaua</i>	Septothecal or partially parathecal	0.01–0.20	Strong	Tied to septa	0.1–0.2	Well-developed; 1–3 rings	Strong banding and dense coenosteum
<i>T. profundata</i>	Septothecal	< 0.1	Strong	Tied to septa	< 0.13	Well-developed; 1–2 rings	No distinct banding
<i>T. raulini</i>	Septothecal	0.04–0.12	Weak	Tied to septa	0.05	Well-developed; 1–2 rings	Sparse density banding
<i>T. reussiana</i>	Septothecal	0.04–0.14	Weak	Free or tied to septa	0.08	Weak; 1 ring	No distinct banding
<i>T. russoi</i>	Septothecal	0.05–0.13	Strong	Tied to septa or free	< 0.15	Well-developed; 2 rings	Strong density banding
<i>T. salentinensis</i>	Septothecal	0.04–0.07	Weak or absent	Free or tied to septa	Not available	Absent	Dense horizontal layering
<i>T. tenera</i>	Septothecal	0.08–0.26	Strong	Tied to septa	0.06–0.15	Weak; 1 ring	Some density banding

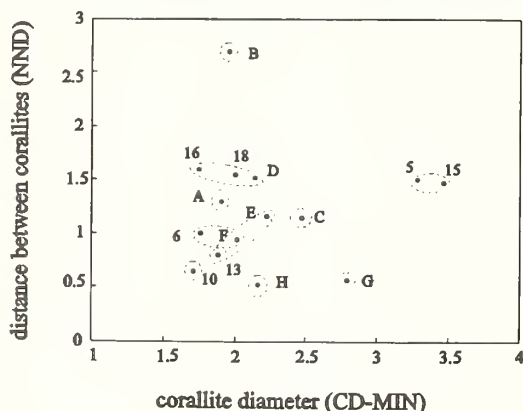
A. Late Oligocene to Early Miocene



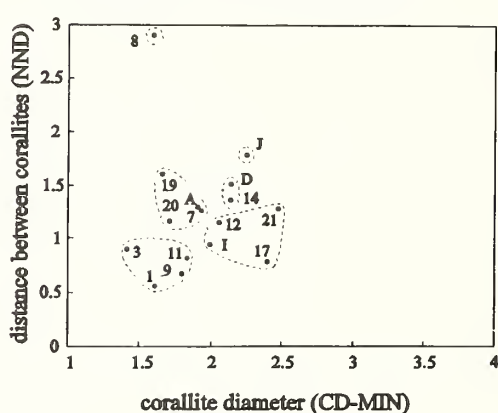
B. Middle to Late Miocene



C. Late Oligocene to Early Miocene



D. Middle to Late Miocene



TEXT-FIG. 11. Plots of mean measurements made on type specimens and statistically recognized species. Dashed lines enclose species that are interpreted to be synonymous. Numbers refer to codes given in Table 8; letters refer to statistically recognized species shown in Text-figures 4, 6 and 8–9. Measurement data for statistically recognized species are given in Appendix 1; measurement data for type specimens are given in Appendix 2.

STRATIGRAPHICAL AND GEOGRAPHICAL DISTRIBUTIONS OF SPECIES

To examine evolutionary patterns within *Tarbellastraea*, we tabulated numbers of colonies of the 12 species occurring in the 13 collecting localities (Table 2) and other type localities (Table 5), and used the results (Table 8) to determine the stratigraphical ranges of species (Text-fig. 12). The genus as a whole appears to have ranged from the Oligocene (Rupelian) to the Early Messinian. Although some authors have suggested that the genus may have originated in the Eocene (e.g. Barta-Calmus 1973; Kuzmicheva 1987), our work clearly shows these earlier occurrences do not belong to the genus *Tarbellastraea* and that the genus most probably originated in the Early Oligocene, as suggested by Chevalier (1962). However, the ranges of most species extend between two or more stages of geological time, and they therefore cannot be considered diagnostic of any one stage (Text-fig. 12; cf. Chevalier 1962). Three possible exceptions are *Tarbellastraea russoi* and *T. salentinensis* which are restricted to the Middle Chattian, and *T. ellisiana* which is restricted to the Lower Burdigalian.

TABLE 8. Occurrences of species of *Tarbellastraea* in the 13 collecting localities used in the morphometric analysis. Locality abbreviations are given in Table 2. Numbers indicate number of non-type colonies examined (Including topotypes). Numbers with 'T's indicate number of primary types examined. E., Early; M., Mid; L., Late.

Locality	<i>abditaxis</i>	<i>bragai</i>	<i>carryensis</i>	<i>chevalieri</i>	<i>distans</i>	<i>ellisiana</i>	<i>profundata</i>
MA	—	1	—	—	—	—	—
AL	—	3	—	—	—	—	—
SI	—	—	—	—	—	—	—
LD	—	—	—	—	—	—	—
BL	—	—	—	—	—	—	—
GR	—	—	—	—	—	—	—
TO	3T	—	—	—	1T	—	—
EG	1T	—	—	—	—	—	—
LP	—	—	2	—	8	10, 1T	—
DX	—	—	—	—	—	10	—
SR	—	—	—	4	—	—	—
NE	—	—	15, 1T	?1T	—	—	1T
SP	—	—	—	—	—	—	—
Other	1T (Granada)	1T (Touraine)	—	—	?1T (Vienna)	—	1T (Vicentin), ?1T (Gaas)

Locality	<i>raulini</i>	<i>reussiana</i>	<i>russoi</i>	<i>salentinensis</i>	<i>tenera</i>	Geological age
MA	—	—	—	—	4	L. Tortonian–?Messinian
AL	—	6	—	—	—	L. Tortonian
SI	1	—	—	—	1, 1T	L. Tortonian
LD	1	12	—	—	—	Langhian
BL	6	4	—	—	1	Langhian
GR	—	5	—	—	—	Langhian
TO	—	1	—	—	4	Burdigalian–Langhian
EG	—	—	—	—	10	E.-M. Burdigalian
LP	7, 2T, ?1T	—	—	—	—	E. Burdigalian
DX	—	—	—	—	—	E. Burdigalian
SR	—	—	—	—	—	L. Chattian–Aquitania
NE	—	—	—	—	—	L. Chattian
SP	—	—	7	1	—	M. Chattian
Other	1T (Malta)	2T, ?1T (Vienna)	—	—	2T (Vienna)	—

Except in the Rupelian, Aquitanian and Messinian, the number of species of *Tarbellastraea* living in the investigated areas during any one time stage ranged from five to seven. Originations of species were concentrated during two time intervals, the Chattian and Burdigalian; while extinctions appear more evenly distributed through time (0–3 species per interval, except the Tortonian). The increase in originations during the Burdigalian was also detected by Chevalier (1962) in his study of the entire reef coral fauna of the western Mediterranean Miocene (86 species, 39 genera), and may have been related to a relatively high global thermal optimum during the Burdigalian (Adams *et al.* 1990; Cahuzac and Chaix 1993; Lauriat-Rage *et al.* 1993; McCall *et al.* 1994). However, unlike Chevalier's (1962) results for the western Mediterranean reef coral fauna as

SPECIES	RUPELIAN	CHATTEAN	AQ.	BURDIGAL.	LAN.	SERRAV.	TORT.	ME.
<i>Tarbellastraea bragai</i>						-----	---	?
<i>Tarbellastraea raulini</i>				=====				-
<i>Tarbellastraea tenera</i>				=====				?
<i>Tarbellastraea reussiana</i>				=====				
<i>Tarbellastraea abditaxis</i>				-----				
<i>Tarbellastraea distans</i>				-----				
<i>Tarbellastraea ellisiana</i>				---				
<i>Tarbellastraea carryensis</i>			=====					
<i>Tarbellastraea chevalieri</i>			=====					
<i>Tarbellastraea russoi</i>		=====						
<i>Tarbellastraea salentinensis</i>		=====						
<i>Tarbellastraea profunda</i>	-----	-----						
total no. of species	1	5	2	7	6	5	5	1
no. of originations	1	4	0	6	1	0	0	0
no. of extinctions	0	3	1	2	1	0	4	1

TEXT-FIG. 12. Stratigraphical range chart summarizing the range interpreted for each species. Solid lines indicate ranges determined by canonical discriminant analysis of thin section measurements. Dashed lines indicate extensions of ranges based on qualitative study of calical surface measurements of primary types.

Column width is proportional to the time duration of each stage.

a whole, our study indicates that there was *not* a progressive increase in species extinctions and decline in species diversity within *Tarbellastraea* as a result of progressive cooling between the Burdigalian and Tortonian. Instead, the species extinction rate remained relatively constant until the latest Miocene (Late Tortonian to Messinian), when five of the 12 species in the genus became extinct within a relatively short interval of time, and Mediterranean reefs became dominated by *Porites* (Esteban 1979; Pomar 1991; Riding *et al.* 1991). Thus, the extinction rate increased in *Tarbellastraea* only after a minimum temperature threshold had been reached as cold Atlantic waters entered the Mediterranean (Esteban 1979).

Cursory examination of the geographical distributions of each species suggests that, although possibly restricted during the Oligocene, the distributions of most species included more than one locality within each time interval, and they were therefore relatively widespread. The oldest occurrence of the genus was *Tarbellastraea profunda* in the Early Oligocene (Rupelian) Castelgomerto Limestone of the Vicentin Southern Alps, the rich coral fauna and 200 m thick barrier reef-lagoonal complex of which have been studied intensively by numerous authors (Pfister

1980; Frost 1981; Bosellini 1988; Bosellini and Russo 1988; Bosellini and Trevisani 1992). During the Late Oligocene (Chattian), four new species arose in the central and western Mediterranean. Like *T. profundata*, the geographical distributions of these four species appear to have been restricted. One of the species (*T. carryensis*) spread to the Aquitaine Basin on the Atlantic coast of France by the Burdigalian, where as many as three new species may have originated. One of the three (*T. distans*) also occurred in the Torino region of Italy, which together with the Vienna Basin also contained three or four new species. The two centres of high diversity in the Aquitaine Basin and Torino region during the Burdigalian were also detected in Chevalier's (1962) study of the whole fauna, in which he reported 96 reef coral species in Aquitaine Basin and 91 reef coral species in Torino. However, it should be noted that reefs in neither of these two regions were thick or well-developed.

During the Mid to Late Miocene, many of the species that arose during the Burdigalian expanded their distributions, especially across the Paratethys as it widened. During the latest Miocene, *Tarbellastraea* was concentrated in the central and western Mediterranean. One new species, *T. bragai*, an important reef-framework builder, may have extended from France to southern Spain.

SYSTEMATIC PALAEOONTOLOGY

As described in previous sections, species have been distinguished in the present study by performing multivariate statistical analyses on measurements of colonies in thin sections that were collected at 13 scattered localities across the northern Mediterranean region (Table 2). As described earlier, these collections were made by: (1) A. F. Budd (deposited at SUI), (2) F. R. Bosellini (deposited at IPUM), (3) J. C. Braga (deposited at SUI), and (4) A. Russo (deposited at IPUM). Several additional colonies in the collections of Chevalier and d'Orbigny (deposited at MNHN, I.P.) were also measured in thin section. All of these measured colonies are listed in the 'Material' sections below. Where applicable, localities for colonies listed in the 'Material' sections are abbreviated as given in Table 2. In some instances, additional unmeasured colonies are also listed in the 'Material' sections. Type specimens (Table 4) have been assigned qualitatively to statistically distinguished species by visual examination and by consideration of a few cursory measurements on calical surfaces (Appendix 2). In the two cases where thin sections of holotypes were available (i.e. *T. carryensis* (MNHN, I.P.-R10521) and *T. aquitaniensis* (MNHN, I.P.-R10518)), thin section measurements have been used to assign type specimens to statistically distinguished species. Except in a few rare instances, only specimens given in Table 4 are listed in synonymies.

The characters treated in 'Diagnosis' and 'Description' sections are summarized in the chart in Table 7. Except in the cases of *T. abditaxis* and *T. profundata*, all descriptions and measurements of corallite level characters are based on examination of thin sections. In general, the range of values given is equal to the overall corallite mean for each species $\pm$ one standard deviation. The total number of corallites measured for each species is given in Appendix 1. The range of values given for columella thickness represents an approximate total range of thickness for this feature. In the qualitative description of dissepiments, 'well-developed' is defined as having a ring of dissepiments extending across more than half a corallite as seen in thin section.

Abbreviations of repository institutions. BSPHGM, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany; IPUM, Istituto di Paleontologia, Università di Modena, Italy; KME, Krahnletzt Museum, Eggenburg, Austria; MGU, Moscow State University, Russia; MNHN, I.P., Muséum National d'Histoire Naturelle, Institut de Paléontologie, Paris, France; MPUP, Museo dell'Istituto di Geologia e Paleontologia, Università di Padova, Italy; MPUR, Museo di Paleontologia, Università di Roma, Italy; NHMW, Naturhistorisches Museum Wien, Vienna, Austria; SUI, Department of Geology, University of Iowa, Iowa City, USA.

Genus *TARBELLASTRAEA* Alloiteau, 1950

Type species. Astrea ellisiana Defrance, 1825, p. 382.

Diagnosis. Plocoid colonies with small, cylindrical or subcylindrical corallites. Septothecate, or partially parathecate in larger corallites. Septa in 3–4 cycles; first cycle distinct, lacking paliform lobes. Columella generally lamellar at calicular surface, sublamellar to lamellar below. Weakly costate with tabulo-vesicular endotheca and exotheca. Endotheca consisting of thin dissepiments arranged in one or two concentric circles near wall.

Remarks. Alloiteau (1950) established *Tarbellastraea* and designated *Astrea ellisiana* Defrance as the type species of the genus. Subsequent detailed diagnoses of the genus appeared in Alloiteau (1952, 1957). The diagnosis used in the present study is essentially the same as that given by Alloiteau (1952, 1957), except that the condition of the corallite wall in the genus is predominantly septothecal in the sense of Vaughan and Wells (1943) and Wells (1956). The holotype of *T. ellisiana* (Defrance) was collected at St-Paul-lès-Dax, and was reported by Alloiteau (1957) as lost. Alloiteau (1957, pl. 8, figs 4, 15) designated a neotype (MNHN, I.P.-R10933), which could not be located at the MNHN, I.P. (S. Barta-Calmus, pers. comm. 1994). Because the potential still exists for this neotype to be found, we hesitate to designate another neotype, and thus base our concept of *T. ellisiana* (Defrance) on the study of 10 'topotype' specimens in the general collections in Paris (MNHN, I.P., AFB # 129, 131, 133–140) labelled as '*Tarbellastraea ellisiana* (Defrance, 1826)' from Mérignac, Gironde, France. These specimens were amongst the material studied by Alloiteau (1957) in designating his neotype, and were also studied by Chevalier (1962).

As noted above, species included in *Tarbellastraea* are most similar to those in the genus *Antiguastrea*. They can generally be distinguished by their more clearly plocoid form, their smaller corallite size and fewer septa. Also, in species of *Tarbellastraea* the first cycle of septa is commonly distinctly thicker and longer than the second cycle, while in *Antiguastrea* the first and second cycles of septa are subequal. *Antiguastrea* species also tend to possess a better developed endotheca than species of *Tarbellastraea*, though this is probably a factor of the generally larger corallite size in *Antiguastrea*.

Tarbellastraea abditaxis Chevalier, 1962

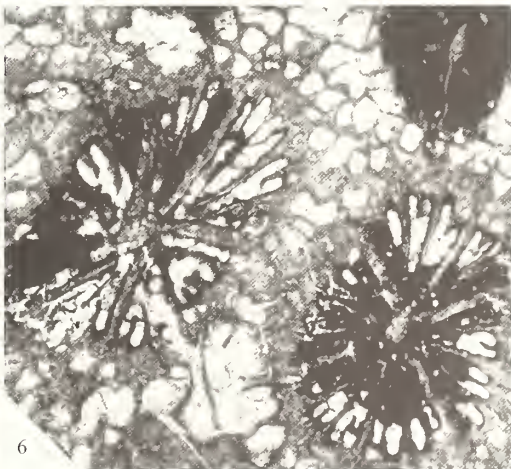
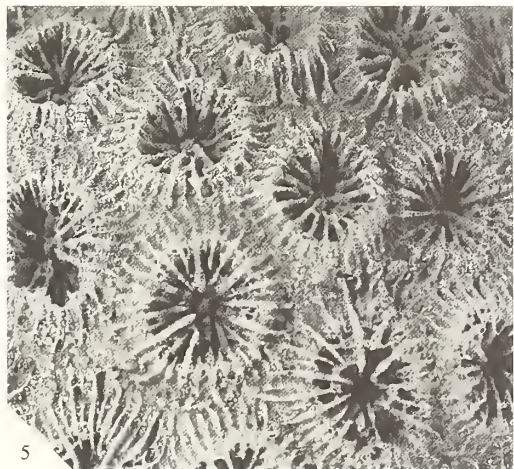
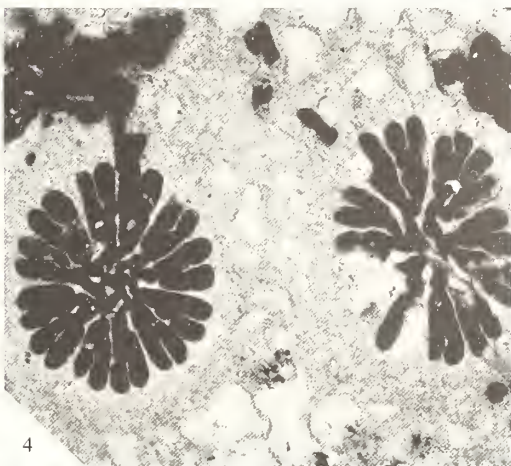
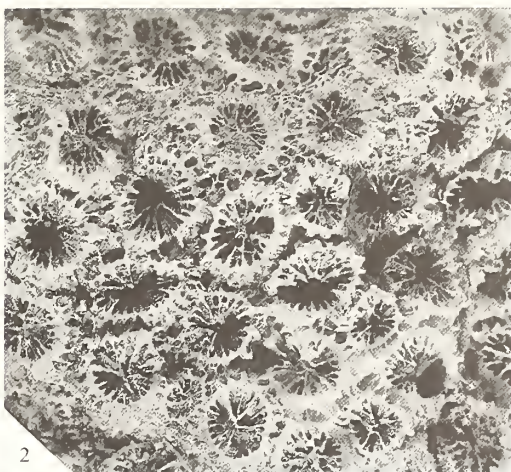
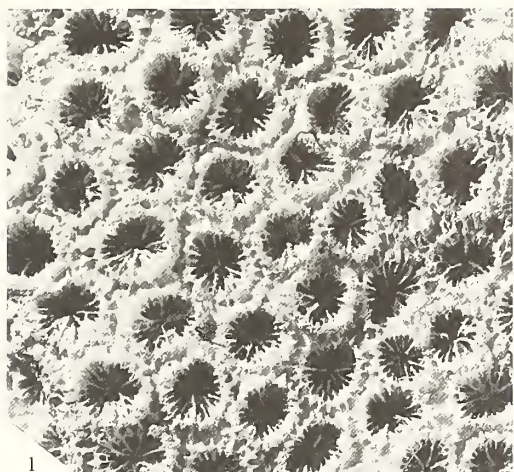
Plate 1, figures 1–2; Text-figures 11–12

- 1925 *Orbicella eggenburgensis* var. *formosa* Kühn, p. 7, pl. 1, fig. 3.
- 1962 *Tarbellastraea abditaxis* Chevalier, p. 204, pl. 6, fig. 10; pl. 23; fig. 8.
- 1962 *Tarbellastraea aquitaniensis* var. *termofuræ* Chevalier, p. 202, pl. 8, figs 17–18.
- 1962 *Tarbellastraea* cf. *eggenburgensis* (Kühn); Chevalier, p. 202, pl. 6, fig. 3; pl. 24, fig. 9.
- 1962 *Tarbellastraea eggenburgensis* var. *andalousiensis* Chevalier, p. 203, pl. 9, fig. 13; pl. 23, fig. 9.

Holotype. MNHN, I.P.-R10525; Sciolze, Torino (Italy); Burdigalian–Langhian.

EXPLANATION OF PLATE 1

- Figs 1–2. *Tarbellastraea abditaxis* Chevalier, 1962; Burdigalian–Langhian, Sciolze, Torino (Italy), calical surfaces. 1, holotype, MNHN, I.P.-R10525. 2, synonym, MNHN, I. P. (original figured specimen of *Tarbellastraea* cf. *eggenburgensis* Chevalier, 1962, pl. 6, fig. 3, and pl. 24, fig. 9). Both $\times 5$.
- Figs 3–4. *Tarbellastraea bragai* Stemmann and Budd sp. nov.; holotype, SU1-84664, Upper Tortonian, Purchena, Almería (Spain). 3, calical surface; $\times 7$. 4, transverse thin section; $\times 11$.
- Figs 5–6. *Tarbellastraea carryensis* (d'Orbigny, 1852); holotype, MNHN, I.P.-R10521, Upper Chattian, Carry-le-Rouet, La Nerthe, Bouches-du-Rhône (France). 5, calical surface; $\times 5$. 6, transverse thin section; $\times 11$.



Material. None, other than the type specimens for the five species given in the synonymies above (see Table 4 for museum catalogue numbers).

Diagnosis. Massive colonies with intermediate-sized, closely spaced corallites bearing a thick wall.

Description. Colony form massive. Corallite round, diameter 1.5–2.3 mm, centres spaced 2.2–3.0 mm apart with 23–25 septa per centre. Length of first cycle septa < 1.1 mm. Largest costae moderately long. Corallite wall septothecal and 0.15–0.25 mm thick. Columella strong or weak, apparently tied to septa, and < 0.08 mm thick. Endotheca weak or absent. Exotheca exhibits no distinct density banding.

Remarks. None of the collections in our study contains specimens of *T. abditaxis*. This species is closest morphologically to *T. chevalieri* and *T. reussiana* (Text-fig. 6). It can be distinguished from the former by its more closely spaced corallites and from the latter by its smaller corallite diameter and its higher number of septa per corallite. This species appears similar to what has been called '*T. eggenburgensis*' by some past authors (e.g. Chevalier 1962). However, the syntypes of *Orbicella eggenburgensis* Kühn, 1925 (pl. 1, figs 1–2) at the KME have a large, spongy columella and clearly belong to *Solenastrea* as defined in Table 1. We interpret the name *Orbicella eggenburgensis* var. *formosa* to be infrasubspecific, because Kühn (1925) originally described this variety as caused by environmental variation and not by geographical variation. Following Article 45 of the International Code of Zoological Nomenclature (Ride *et al.* 1985, p. 85), the valid name is, therefore, *Tarbellastraea abditaxis* Chevalier, 1962.

Occurrence. Lower–Middle Burdigalian, Eggenburg (Austria); Burdigalian–Langhian, Torino (Italy); Tortonian, Granada (Spain).

Tarbellastraea bragai Stemann and Budd sp. nov.

Plate 1, figures 3–4; Text-figures 6–7, 9, 11–12

?1962 *Tarbellastraea ellisiana* var. *manthelensis* Chevalier, p. 195, pl. 5, fig. 4 [not seen].

Derivation of name. In honour of Juan C. Braga (Departamento de Estratigrafía y Paleontología, Universidad de Granada, Spain).

Holotype. SUI-84664; Purchena, Almería (Spain); Upper Tortonian.

Paratypes. SUI-84658, 84659; Purchena, Almería (Spain); Upper Tortonian.

Material. 9 SUI colonies (AL), 3 measured: SUI-84658–84659, 84664; one measured IPUM specimen (MA): IPUM-24880.

Diagnosis. Laminar, columnar or branched colonies with intermediate-sized, widely spaced corallites.

Description. Colony form laminar, columnar or branched palmately. Corallite shape irregular, diameter 1.8–2.3 mm, centres spaced 3.4–4.7 mm apart with 23–25 septa per centre. Length of first cycle septa 0.87–1.11 mm. Length of largest costae 0.39–0.53 mm. Corallite wall septothecal and 0.09–0.19 mm thick. Columella strong or weak, tied to septa, and 0.05–0.13 mm thick. Endotheca weak or absent. Exotheca exhibits dense, horizontal layering.

Remarks. One specimen of *T. ellisiana* var. *manthelensis* from Manthelon (France) in the d'Orbigny collection at MNHN, I.P. (R10509) belongs to this species, but it does not match the photograph of the type given by Chevalier (1962, pl. 5, fig. 4), nor do measurements made in the present study match those given for this variety by Chevalier (1962). Therefore, *T. ellisiana* var. *manthelensis* is only questionably synonymized. *T. bragai* is closest morphologically to *T. raulini*

and to *T. reussiana* (Text-fig. 6). It can be readily distinguished from these two species by its more widely spaced corallites, and its growth form.

Occurrence. Langhian, Manthelan, Touraine, Indre-et-Loire (France); Upper Tortonian, Almería (Spain); Upper Tortonian–?Lower Messinian, Mallorca (Spain).

Tarbellastraea carryensis (d'Orbigny, 1852)

Plate 1, figures 5–6; Text-figures 4–5, 8, 11–12

1852 *Phyllocoenia carryana* d'Orbigny, p. 147.

Holotype. MNHN, I.P.-R10521. Carry-le-Rouet, La Nerthe, Bouches-du-Rhône (France); Upper Chattian. Thin section measured.

Material. 69 SUI colonies (NE), 14 measured; SUI-84764–84765, 84767–84768, 84782, 84786, 84788–84790, 84795, 84797, 84804, 84807–84808. Two non-type specimens (Mérignac, Gironde, France) at MNHN, I.P. measured (AFB # 130, 132). One topotype (La Nerthe, Bouches-du-Rhône, France) in the Chevalier collection at MNHN, I.P. measured (AFB # 171).

Diagnosis. Irregularly shaped colonies with large, widely spaced corallites.

Description. Colony form massive–columnar. Corallite shape irregular, diameter 2.1–2.9 mm, centres spaced 3.1–4.1 mm apart with 26–33 septa per centre. Length of first cycle septa 0.86–1.16 mm. Length of largest costae 0.42–0.62 mm. Corallite wall septothecal or partially parathecal and 0.02–0.16 mm thick. Columella strong or weak, tied to septa, and < 0.14 mm thick. Endotheca well-developed forming 1–3 rings. Exotheca exhibits no distinct density banding.

Remarks. *T. carryensis* is closest morphologically to *T. raulini* and *T. ellisiana* (Text-fig. 4). It can be distinguished from the former primarily by its higher number of septa per corallite and from the latter by its larger corallite size, its reduced costae, and its slightly fewer number of septa per corallite.

Occurrence. Upper Chattian, La Nerthe, Bouches-du-Rhône (France); Lower Burdigalian, Bordeaux (France).

Tarbellastraea chevalieri Bosellini sp. nov.

Plate 2, figures 1–2; Text-figures 8, 11–12

?1962 *Tarbellastraea carryensis* var. *minor* Chevalier, p. 198, pl. 10, figs 3, 9–10.

Derivation of name. In honour of the late J. P. Chevalier (MNHN, I.P.).

Holotype. IPUM-24876; Dolianova, Sardinia (Italy); Upper Chattian–Aquitanian.

Paratypes. IPUM-24877–24879; Dolianova, Sardinia (Italy); Upper Chattian–Aquitanian.

Material. 4 IPUM colonies (SR), 4 measured: IPUM-24876–24879; plus type specimen of *T. carryensis* var. *minor* (MNHN, I.P.-R10522).

Diagnosis. Massive colonies with small, intermediately spaced corallites bearing a thick wall.

Description. Colony form massive. Corallite shape round–irregular, diameter 1.6–2.4 mm, centres spaced 2.5–3.4 mm apart with 19–25 septa per centre. Length of first cycle septa 0.66–0.94 mm. Largest costae relatively short. Corallite wall septothecal and 0.09–0.29 mm thick. Columella weak or absent, tied to septa, and 0.05–0.09 mm thick. Endotheca weak or absent. Exotheca exhibits no distinct density banding.

Remarks. The specimens from Sardinia have a distinctively thicker wall and more reduced columella than *Tarbellastraea carryensis* var. *minor* Chevalier, 1962. Thus, the Sardinian specimens and *T. carryensis* var. *minor* are only questionably synonymized. Furthermore, following Article 16 of the International Code of Zoological Nomenclature (Ride *et al.* 1985, p. 38), a scientific name proposed for a variety after 1960 is excluded from zoological nomenclature. A new name is therefore assigned to the species. The reduced costae of the Sardinian specimens suggest that this species may be allied with *Solenastrea*. However, because of its reduced columella, the species is assigned to *Tarbellastraea*, until a more thorough phylogenetic study can be performed.

T. chevalieri is extremely close morphologically to *T. abditaxis* and is distinguished primarily by its more widely spaced corallites (Text-fig. 11). More samples from the Torino region of Italy need to be evaluated in order to determine whether *T. chevalieri* and *T. abditaxis* are truly distinct. *T. chevalieri* is also close morphologically to *T. tenera* (Text-fig. 8) from which it differs primarily in its larger, more narrowly spaced corallites.

Occurrence. ?Upper Chattian, La Nerthe, Bouches-du-Rhône (France); Upper Chattian–Aquitanian, Sardinia (Italy).

Tarbellastraea distans Chevalier, 1962

Plate 2, figure 6; Text-figures 4–5, 9, 11–12

?1847 *Explanaria crassa* Reuss, p. 18, pl. 3, fig. 1.

1962 *Tarbellastraea distans* Chevalier, p. 208, pl. 5, fig. 9 [not seen].

Holotype. MNHN, I.P.-R55165; Albugnano, Torino (Italy); Burdigalian–Langhian (could not be found).

Material. 7 SUI colonies (LP), 6 measured: SUI-51236, 51243, 51251, 51255, 51257–51258. Two non-type specimens (Le Peloua, Gironde, France) in the Chevalier collection at MNHN, I.P. measured (AFB# 117, 160). Holotype of *Explanaria crassa* (NHMW-1832.I.1368).

Diagnosis. Massive colonies with small, very widely spaced corallites bearing long costae.

Description. Colony form massive. Corallite round, diameter 1.7–2.1 mm, centres spaced 4.1–5.2 mm apart with 23–26 septa per centre. Length of first cycle septa 0.68–0.84 mm. Length of largest costae 0.49–0.79 mm. Corallite wall septothecal and 0.05–0.21 mm thick. Columella weak, free or tied to septa, and < 0.08 mm thick. Endotheca well-developed forming one ring. Exotheca exhibits strong density banding.

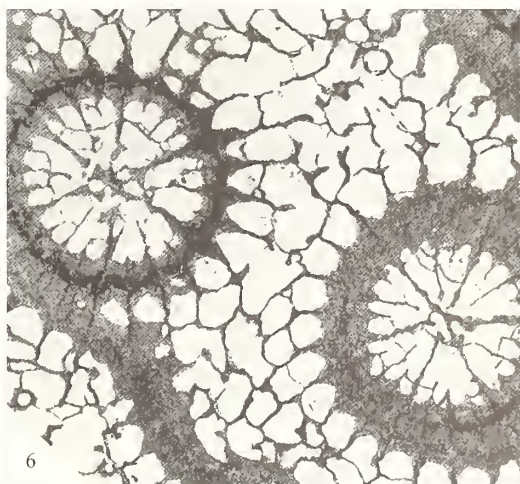
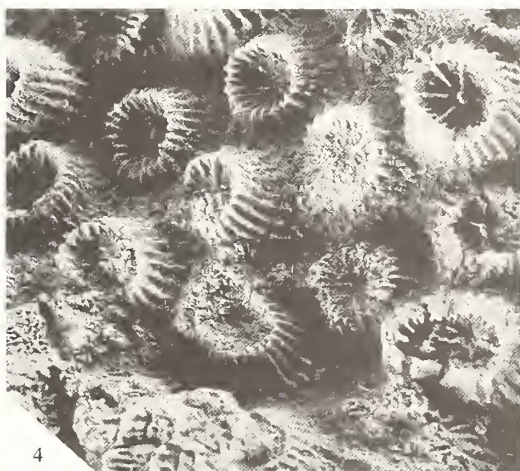
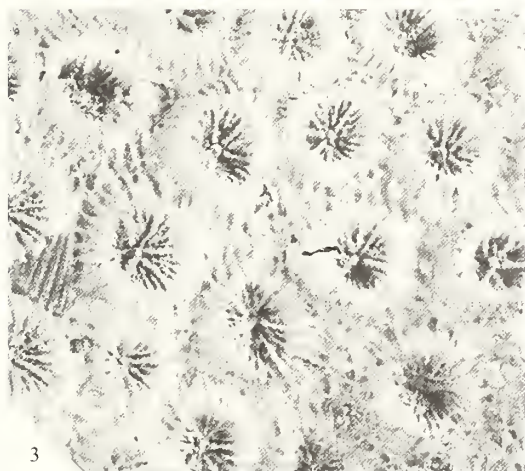
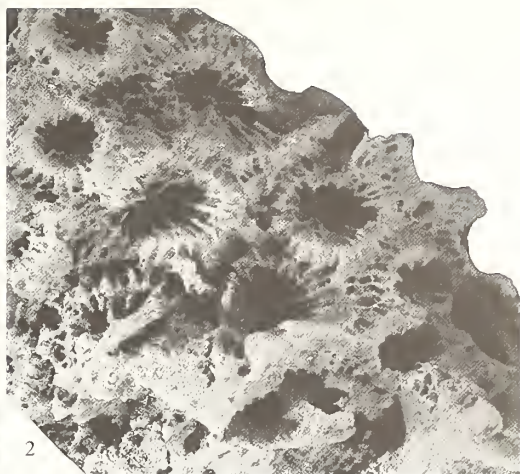
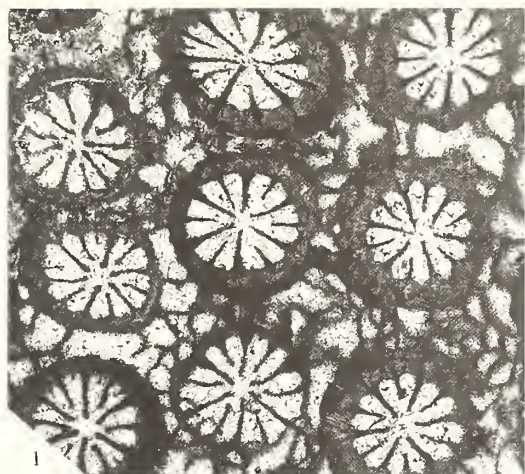
Remarks. *Explanaria crassa* is only questionably synonymized with this species, because of the poor preservation of its holotype (NHMW-1832.I.1368). *T. distans* differs from all other members of

EXPLANATION OF PLATE 2

Figs 1–2. *Tarbellastraea chevalieri* Bosellini sp. nov. 1, holotype, IPUM-24876; Upper Chattian–Aquitanian, Dolianova, Sardinia (Italy); transverse thin section; $\times 10$. 2, possible synonym, MNHN, I.P.-R10522 (holotype of *Tarbellastraea carryensis* var. *minor* Chevalier, 1962); Upper Chattian, Carry-le-Rouet, La Nerthe, Bouches-du-Rhône (France); calical surface; $\times 5$.

Figs 3–5. *Tarbellastraea tenera* (Reuss, 1847); calical surfaces. 3, synonym, NHMW-1854.XXXV.500 (holotype of *Heliastraea conoidea* Reuss, 1872); Badenian (Langhian), Enzesfeld (Austria); $\times 5$. 4, synonym, MNHN, I.P.-R10522 (holotype of *Tarbellastraea siciliae* Chevalier, 1962); Upper Tortonian, Landro, Sicily (Italy); $\times 5$. 5, holotype, NHMW-1872.XIII.61; Badenian (Langhian), Kostel, Vienna Basin (Austria); $\times 6$.

Fig. 6. *Tarbellastraea distans* Chevalier, 1962; non-type, MNHN, I.P., AFB# 117; Lower Burdigalian, Le Peloua, Bordeaux (France); transverse thin section; $\times 11$.



Tarbellastraea in its extremely widely spaced corallites (Text-fig. 5). It is closest morphologically to *T. raulini*.

Occurrence. Lower Burdigalian, Bordeaux (Gironde, France); Burdigalian–Langhian, Torino (Italy); ?Langhian, Vienna (Austria).

Tarbellastraea ellisiana (Defrance, 1826)

Plate 3, figures 1–2; Text-figures 1, 4–5, 8, 11–12

1826 *Astrea ellisiana* Defrance, p. 382 [holotype lost].

1957 *Tarbellastraea ellisi* (Defrance, 1926); Alloiteau, p. 128, pl. 8, fig. 4, 15 [neotype designated, not seen].

?1962 *Tarbellastraea mimbastensis* Chevalier, p. 199, pl. 5, fig. 3; pl. 23, fig. 1.

Neotype. MNHN I.P.-R10933; Mérignac, Gironde, Bordeaux (France); Lower Burdigalian (could not be found).

Material. 10 SUI colonies (DX), all measured: SUI-84734–84743. Ten topotypes (Mérignac, Gironde, France) at MNHN, I.P. measured (AFB # 129, 131, 133–140). Holotype of *T. mimbastensis* (MNHN, I.P.-R10529).

Diagnosis. Massive colonies with intermediate-sized to large, intermediately spaced, irregularly shaped corallites bearing numerous septa.

Description. Colony form massive. Corallite shape irregular, diameter 1.9–2.5 mm, centres spaced 2.9–3.9 mm apart with 27–35 septa per centre. Length of first cycle septa 0.69–1.01 mm. Length of largest costae 0.47–0.77 mm. Corallite wall septothecal or partially parathecal and 0.01–0.20 mm thick. Columella strong, tied to septa, and 0.1–0.2 mm thick. Endotheca well-developed forming 1–3 rings. Exotheca exhibits strong density banding and dense coenosteum.

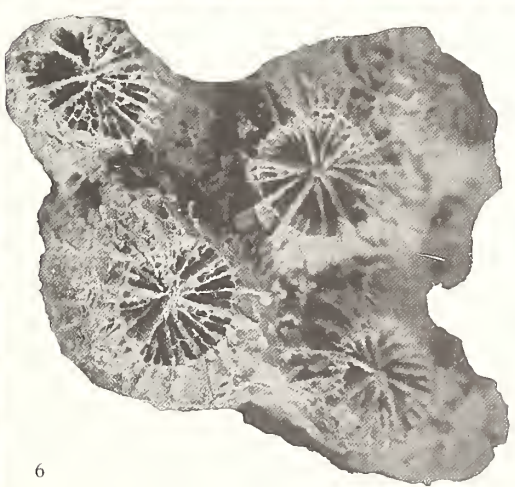
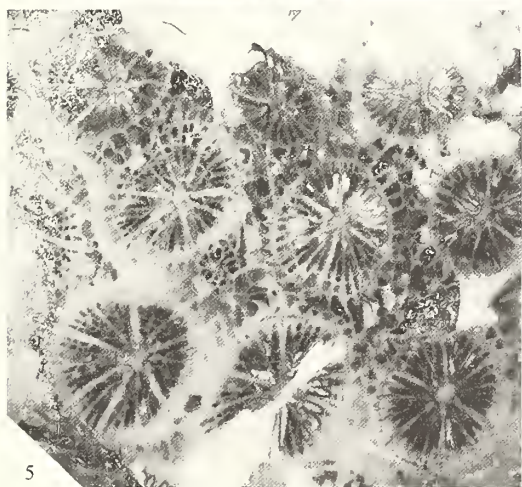
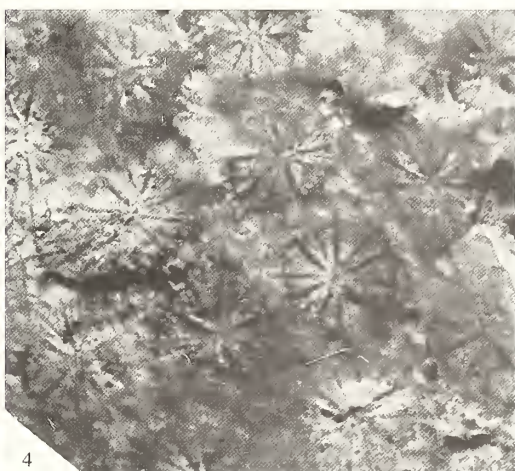
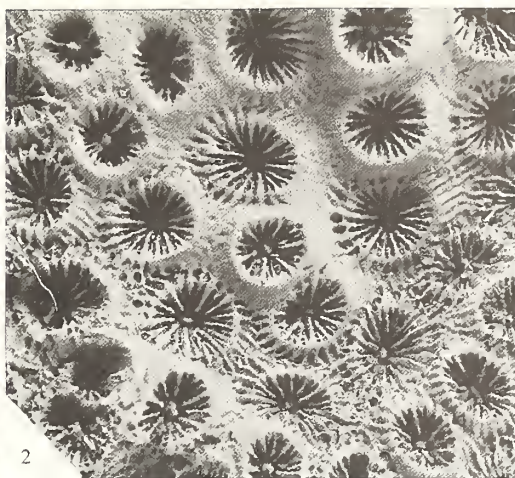
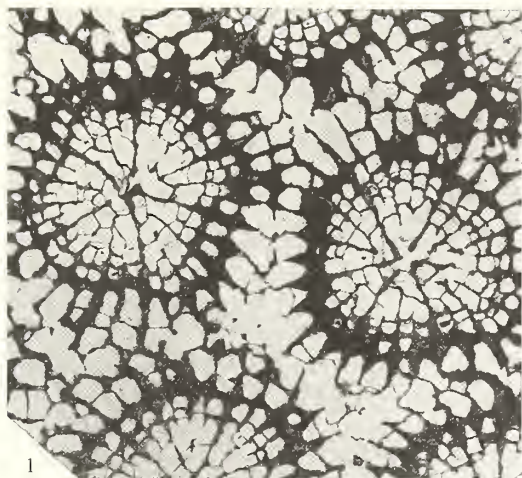
Remarks. The holotype is lost, and the specimen that was figured in Alloiteau (1957, pl. 8, fig. 4, 15) and used in Alloiteau's original description of the genus *Tarbellastraea* is considered to be the neotype [S. Barta-Calmus, pers. comm. 1994]. The neotype could not be found at the MNHN, I.P. for our study; however, ten topotypes that are morphologically similar to Alloiteau's (1957) description and photograph were measured in thin section and included in the statistical analyses. As explained in the main text, *T. mimbastensis* is only questionably synonymized because of its slightly smaller corallite diameter and fewer number of septa. *T. ellisiana* is very close morphologically to *T. carryensis* (Text-fig. 4), but can be distinguished by its smaller corallite size, more numerous septa per corallite, and better developed costae.

Occurrence. Lower Burdigalian, Saint-Paul-les-Dax, Landes and Bordeaux, Gironde (France).

EXPLANATION OF PLATE 3

Figs 1–2. *Tarbellastraea ellisiana* (Defrance, 1826); Lower Burdigalian. 1, topotype, MNHN, I.P.; Mérignac, Gironde, Bordeaux (France); transverse thin section; $\times 11$. 2, possible synonym, MNHN, I.P.-R10529 (holotype of *Tarbellastraea mimbastensis* Chevalier, 1962); Mimbaste, Bordeaux (France); calical surface; $\times 5$.

Figs 3–6. *Tarbellastraea profundata* (Catullo, 1856); calical surfaces. 3–4, holotype, MPUP-8142, Rupelian, Montecchio, Vicenza (Italy). 5, synonym, MNHN, I.P.-R10523 (holotype of *Tarbellastraea carryensis* var. *major* Chevalier, 1962); Upper Chattian, Carry-le-Rouet, La Nerthe, Bouches-du-Rhône (France). 6, possible synonym, MNHN, I.P.-M00787 (non-type specimen of *Tarbellastraea edwardsi* Chevalier, 1956 (= *Phyllocoenia archiaci* Milne Edwards and Haime, 1848)), Stampian, Gaas, Landes (France). All $\times 5$.



Tarbellastraea profundata (Catullo, 1856)

Plate 3, figures 3–6; Text-figures 11–12

- 1856 *Astrea profundata* Catullo, p. 56, pl. 11, fig. 6.
 ?1955 *Tarbellastraea edwardsi* Chevalier, p. 390, pl. 3, fig. 4 [= *Phyllocoenia archiaci* Milne Edwards and Haime 1848, p. 303].
 1962 *Tarbellastraea carryensis* var. *major* Chevalier, p. 198, pl. 7, fig. 8.
 1980 *Tarbellastraea anomala* (Michelotti); Pfister, p. 78, pl. 12, figs 1–2.
 ?1985 *Tarbellastraea* cf. *profundata* (Catullo); Pfister, p. 197 [not seen].

Holotype. MPUP-8142; Montecchio, Vicenza (Italy); Rupelian.

Material. None other than the type specimens for the first three species given in the synonymies above (see Table 4 for museum catalogue numbers), and Pfister's (1980) specimen of '*T. anomala*' (Pfister collection, Naturhistorisches Museum Bern, Switzerland, Pf-SL 12/1-2).

Diagnosis. Irregularly shaped colonies with very large, widely spaced corallites bearing numerous septa.

Description. Colony form massive-digitate. Corallite shape round, diameter 3.3–3.5 mm, centres spaced 4.8–5.0 mm apart with 36–39 septa per centre. Length of first cycle septa 1.2–1.6 mm. Largest costae moderately long. Corallite wall septothecal and < 0.1 mm thick. Columella strong, tied to septa, and < 0.13 mm thick. Endotheca well-developed forming 1–2 rings. Exotheca exhibits no distinct density banding.

Remarks. None of the collections in our study contains specimens of *T. profundata*. This species can be distinguished easily from all other members of the genus by its extremely large corallite diameters and extremely high number of septa per corallite (Text-fig. 11). A photograph of one type specimen (Pl. 3, fig. 6) of *T. edwardsi* from the Stampian of Gaas (Landes, France) has been examined (S. Barta-Calmus, pers. comm. 1993), but it does not match the photograph given in Chevalier (1955, pl. 3, fig. 4), nor does the photo correspond with measurements given by Chevalier (1955). Therefore, *T. edwardsi* is only questionably synonymized pending examination of more material from Gaas.

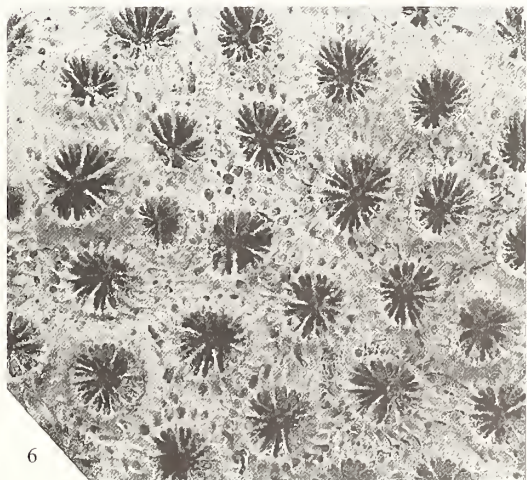
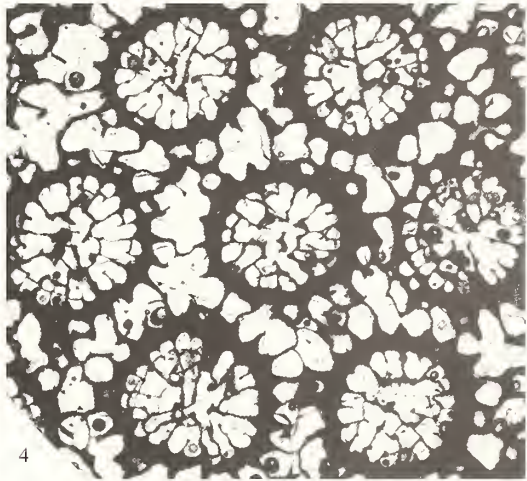
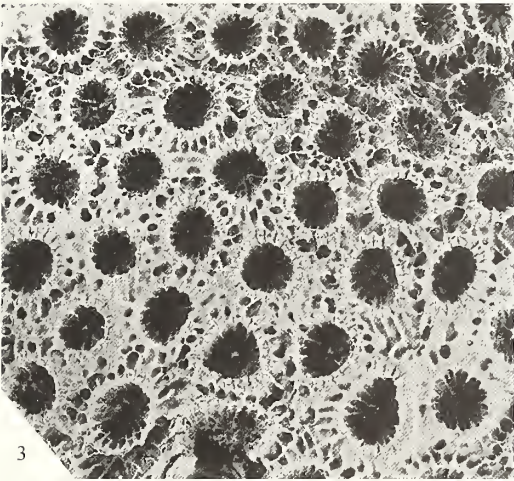
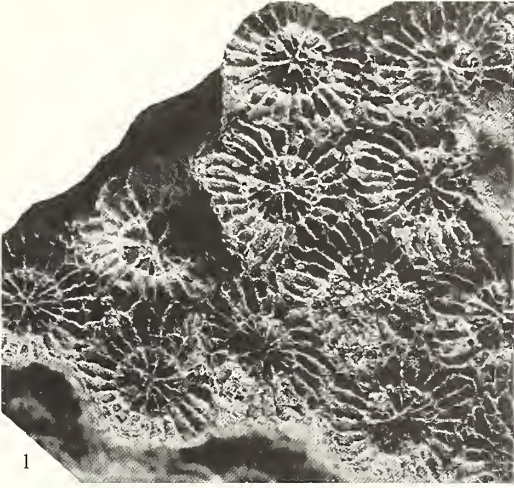
Pfister's (1980) specimen of '*T. anomala*' from San Luca (Vicenza, Italy) has a sublamellar columella and weakly developed paliform lobes, two diagnostic features of *Tarbellastraea* (Table 1), and differs considerably from the holotype of *Leptastraea anomala* Michelotti, 1871 (MPUR 3302), which has a well-developed spongy columella (Text-fig. 10). It has a corallite size and spacing similar to those of *T. profundata*. Therefore, we synonymize it with *T. profundata*. Pfister (1985) also described one colony of *T. cf. profundata* from the Rupelian near Cairo Montenotte (Liguria, Italy); however, this specimen is reported to have significantly smaller calices (2–2.5 mm) and can therefore only be questionably assigned to *T. profundata*.

Occurrence. Rupelian, Vicenza (Italy); Upper Chattian, La Nerthe, Bouches-du-Rhône (France).

EXPLANATION OF PLATE 4

Figs 1–4. *Tarbellastraea raulini* (Milne Edwards and Haime, 1850); Lower Burdigalian, Le Peloua, Bordeaux (France). 1, holotype, MNHN, I.P.-M01281; calical surface; $\times 5$. 2, possible synonym, MNHN, I.P.-R10518 (holotype of *Tarbellastraea aquitaniensis* Chevalier, 1962); calical surface; $\times 5$. 3–4, synonym, MNHN, I.P.-M01184 (holotype of *Tarbellastraea prevostiana* (Milne Edwards and Haime, 1850)). 3, calical surface; $\times 5$. 4, transverse thin section; $\times 11$.

Figs 5–6. *Tarbellastraea reussiana* (Milne Edwards and Haime, 1850); calical surfaces. 5, holotype, NHMW-1846.37.967; Badenian (Langhian), Mattersdorf, Vienna Basin (Austria). 6, figured specimen (Reuss 1872, pl. 9, fig. 2), NHMW-1863.XV.A; Badenian (Langhian), Niederleis, Vienna Basin (Austria). Both $\times 5$.



Tarbellastraea raulini (Milne Edwards and Haime, 1850)

Plate 4, figures 1–4; Text-figures 4, 6–9, 11–12

- 1850 *Astrea raulini* Milne Edwards and Haime, p. 110.
 1850 *Astrea prevostiana* Milne Edwards and Haime, p. 110.
 ?1962 *Tarbellastraea aquitaniensis* Chevalier, p. 201, pl. 9, fig. 12; pl. 23, fig. 2.
 1962 *Tarbellastraea reussiana* var. *echinulata* Chevalier, p. 206, pl. 5, fig. 18; pl. 24, fig. 7.

Holotype. MNHN, I.P.-M01281; Le Peloua, Gironde (France); Lower Burdigalian.

Material. 12 SUI colonies, 10 measured (4LP, 6BL): SUI-51234, 51247–51248, 51253, 84667–84668, 84670–84672, 84674. Three topotypes (Le Peloua, Gironde, France) in the Chevalier collection at MNHN, I.P. measured (AFB# 116, 169, 177). Three non-type specimens (two from Sicily; one from Serière, France) in the Chevalier collection at MNHN, I.P. measured (AFB# 127, 164, 111). Type specimens for the four species given in the synonymies above (see Table 4 for museum catalogue numbers).

Diagnosis. Massive colonies with small to intermediate-sized, widely corallites bearing a thin wall.

Description. Colony form massive. Corallite shape regular, diameter 1.6–2.3 mm, centres spaced 3.0–4.2 mm apart with 23–25 septa per centre. Length of first cycle septa 0.75–0.97 mm. Length of largest costae 0.39–0.63 mm. Corallite wall septothecal and 0.04–0.12 mm thick. Columella weak, tied to septa, and 0.05 mm thick. Endotheca well-developed forming 1–2 rings. Exotheca exhibits sparse density banding.

Remarks. *T. aquitaniensis* is only questionably synonymized because of its more closely spaced corallites with high numbers of septa. *T. raulini* is closest morphologically to *T. tenera* and *T. carryensis* (Text-fig. 4). It can be distinguished from the former by its more widely spaced corallites, and from the latter by its smaller corallites and fewer septa per corallite. *T. aquitaniensis* is only questionably indicated in synonymy with *T. raulini* because its holotype lies within the margin of overlap between *T. raulini* and *T. carryensis*. Because the holotype of *T. aquitaniensis* lies closer to the centre of the *T. raulini* cluster (Text-fig. 4), it more probably belongs to *T. raulini* than to *T. carryensis*.

Occurrence. Lower Burdigalian, Bordeaux, Gironde (France); Langhian, Pleven (Bulgaria), Languedoc (France); Upper Tortonian, Sicily (Italy); Upper Tortonian–Lower Messinian, Malta.

Tarbellastraea reussiana (Milne Edwards and Haime, 1850)

Plate 4, figures 5–6; Plate 5, figures 1–12; Text-figures 6–7, 9, 11–12

- 1847 *Explanaria astroites* (Goldfuss, 1826); Reuss, p. 17, pl. 2, figs 7–8.
 1850 *Astraea reussiana* Milne Edwards and Haime, p. 110.
 1872 *Solenastraea manipulata* Reuss, p. 243, pl. 8, fig. 2.
 1872 *Heliastrea reussiana* Milne Edwards and Haime; Reuss, p. 240, pl. 9, fig. 2; pl. 18, fig. 4.
 ?1925 *Orbicella transsylvanica* Kühn, p. 4.

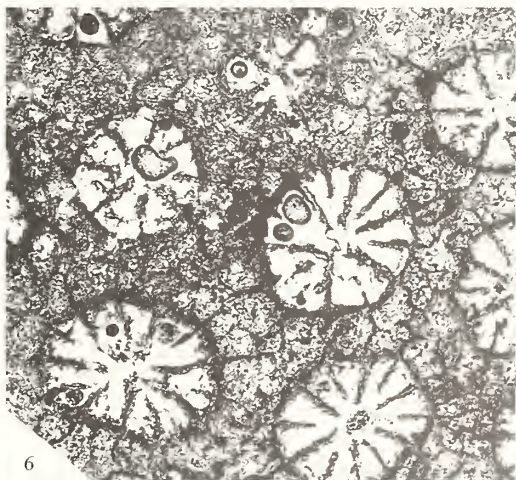
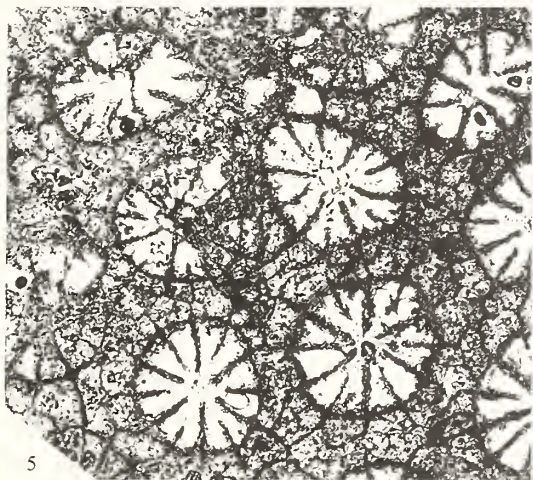
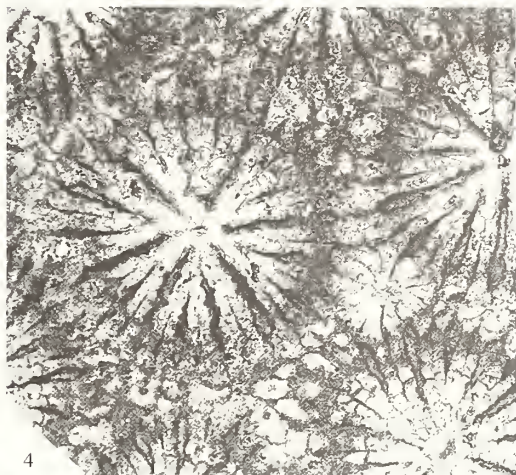
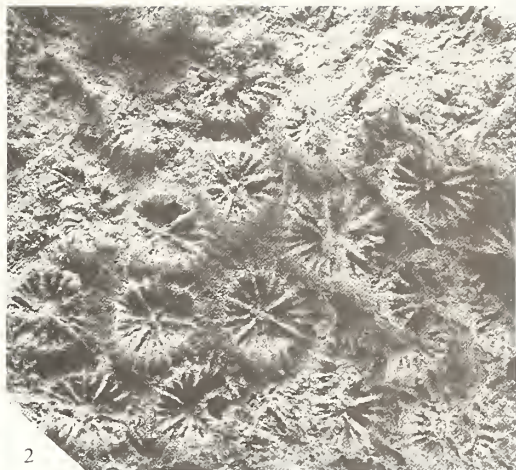
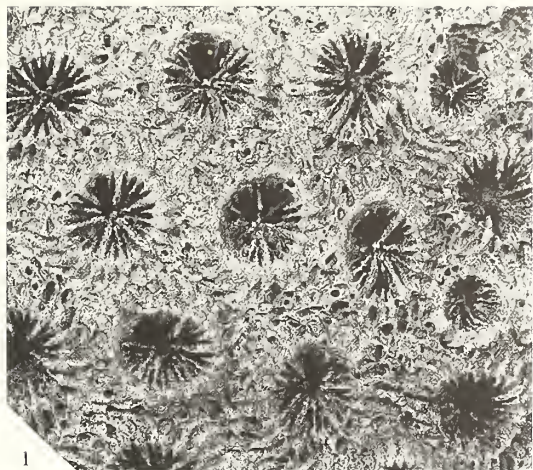
Holotype. NHMW-1846.37.967; Mattersdorf (Austria); Badanian (Langhian).

EXPLANATION OF PLATE 5

Figs 1–2. *Tarbellastraea reussiana* (Milne Edwards and Haime, 1850); calical surfaces. 1, synonym, NHMW-1872.XIII.56 (holotype of *Orbicella transsylvanica* Kühn, 1925); Badanian (Langhian), Lapugy, Vienna Basin (Austria). 2, figured specimen (Chevalier, 1962, pl. 10, fig. 1; pl. 24, fig. 4); MNHN, I.P., Langhian, Autignac, Languedoc (France). Both $\times 5$.

Figs 3–4. *Tarbellastraea russoi* Bosellini sp. nov.; holotype, IPUM-24869; Middle Chattian, Castro Limestone, Vitigliano, Salento (Italy); transverse thin sections; $\times 10$.

Figs 5–6. *Tarbellastraea salentinensis* Bosellini sp. nov.; holotype, IPUM-24868; Middle Chattian, Castro Limestone, Vitigliano, Salento (Italy); transverse thin sections; $\times 10$.



Material. 48 SUI colonies, 26 measured (4BL, 11LD, 5GR, 6AL): SUI-84651–84652, 84655, 84662–84663, 84665–84666, 84675, 84677–84680, 84683, 84687–84688, 84690–84691, 84696, 84702–84706, 84709, 84711, 84715. Two non-type specimens (one Autignac, France; one Sciolze, Italy) in the Chevalier collection at MNHN, I.P. measured (AFB# 100, 179). Type specimens for the four species given in the synonymies above (see Table 4 for museum catalogue numbers) and a specimen figured by Reuss (1872, pl. 9, fig. 2, NHMW-1863.XV.A).

Diagnosis. Irregularly shaped colonies with small, closely spaced corallites bearing a thin wall and short costae.

Description. Colony form massive, knobby. Corallite shape round-irregular, diameter 1.7–2.1 mm, centres spaced 2.5–3.3 mm apart with 23–25 septa per centre. Length of first cycle septa 0.67–0.87 mm. Length of largest costae 0.32–0.47 mm. Corallite wall septothecal and 0.04–0.14 mm thick. Columella weak, free or tied to septa, and 0.08 mm thick. Endotheca weak. Exotheca exhibits no distinct density banding.

Remarks. Milne Edwards and Haime (1850) based their description of *T. reussiana* on Reuss' (1847) specimen of *Explanaria astroites* (Goldfuss) which is currently deposited at NHMW. *Orbicella transylvanica* is only questionably synonymized because of its relatively large corallite diameter. *T. reussiana* is most similar morphologically to *T. tenera* but can be distinguished by its larger, more closely spaced, thin walled corallites (Text-fig. 6).

Occurrence. Burdigalian–Langhian, Torino (Italy); Langhian, Leibnitz and Vienna (Austria), Pleven (Bulgaria), Languedoc (France); Upper Tortonian, Almería (Spain).

Tarbellastraea russoi Bosellini sp. nov.

Plate 5, figures 3–4; Text-figures 8, 11–12

Derivation of name. In honour of Antonio Russo (Istituto di Paleontologia, Università degli Studi di Modena, Italy).

Holotype. IPUM-24869; Vitigliano, Salento (Italy); Middle Chattian.

Paratypes. IPUM-24870–24875; Vitigliano, Salento (Italy); Middle Chattian.

Material. Seven IPUM measured colonies (SP): IPUM-24869–24875.

Diagnosis. Irregularly shaped colonies with large, intermediate- to widely spaced corallites bearing numerous septa.

Description. Colony form massive, knobby. Corallite shape round-irregular, diameter 2.3–3.3 mm, centres spaced 2.7–4.1 mm apart with 30–37 septa per centre. Length of first cycle septa 0.88–1.24 mm. Length of largest costae moderately long. Corallite wall septothecal and 0.05–0.13 mm thick. Columella strong, tied to septa or free, and < 0.15 mm thick. Endotheca well-developed forming two rings. Exotheca exhibits strong density banding.

Remarks. *T. russoi* is similar morphologically to *T. carryensis*, but can easily be distinguished by its larger corallites and its more numerous septa (Text-fig. 8).

Occurrence. Middle Chattian, Salento (Italy).

Tarbellastraea salentinensis Bosellini sp. nov.

Plate 5, figures 5–6; Text-figures 8, 11

Derivation of name. After the Salento Peninsula, the type locality.

Holotype. IPUM-24868; Vitigliano, Salento (Italy); Middle Chattian.

Material. One measured colony (SP): the holotype.

Diagnosis. Irregularly shaped colonies with intermediate-sized, closely spaced corallites bearing very few septa.

Description. Colony form massive-digitate. Corallite shape irregular, diameter 1.8–2.5 mm, centres spaced 2.6–2.8 mm apart with 15–22 septa per centre. Length of first cycle septa 0.70–0.86 mm. Length of largest costae relatively short. Corallite wall septothecal and 0.04–0.07 mm thick. Columella weak or absent, free or tied to septa, and 0.06–0.09 mm thick. Endotheca absent. Exotheca exhibits dense, horizontal layering.

Remarks. *T. salentinensis* is clearly distinct from all other members of the genus in its reduced number of septa per corallite and its more narrowly spaced corallites (Text-figs 8, 11).

Occurrence. Middle Chattian, Salento (Italy).

Tarbellastraea tenera (Reuss, 1847)

Plate 2, figures 3–5; Text-figures 4–9, 11–12

1847 *Explanaria tenera* Reuss, p. 18, pl. 3, fig. 2.

1872 *Heliastrea conoidea* Reuss, p. 240, pl. 10, fig. 3.

1962 *Tarbellastraea siciliae* Chevalier, p. 207, pl. 7, fig. 10; pl. 23, fig. 7.

Holotype. NHMW-1872. XIII.61; Kostel (Austria); Badenian (Langhian).

Material. 19 SUI colonies (EG), 11 measured: SUI-84673, 84716–84720, 84724–84725, 84727, 84731–84732; 4 IPUM specimens (MA), 4 measured: IPUM-24881–24884. Five non-type specimens (four from Torino, Italy; one from Sicily) in the Chevalier collection at MNHN, I.P. measured AFB # 43, I61–I63, I65. Type specimens for the three species given in the synonymies above (see Table 4 for museum catalogue numbers).

Diagnosis. Columnar colonies with small, intermediately spaced corallites bearing a thick wall.

Description. Colony form massive columnar. Corallite shape round irregular, diameter 1.6–2.0 mm, centres spaced 2.7–3.7 mm apart with 23–25 septa per centre. Length of first cycle septa 0.63–0.79 mm. Length of largest costae 0.42–0.78 mm. Corallite wall septothecal and 0.08–0.26 mm thick. Columella strong, tied to septa, and 0.06–0.15 mm thick. Endotheca weak to well-developed forming one ring. Exotheca exhibits some density banding.

Remarks. *T. tenera* is closest morphologically to *T. raulini* and *T. reussiana* (Text-fig. 6). It can readily be distinguished from these two species by its slightly smaller corallites and its thicker wall.

Occurrence. Lower Burdigalian, Eggenburg (Austria); Burdigalian–Langhian, Torino (Italy); Langhian, Pleven (Bulgaria); Upper Tortonian, Sicily (Italy); Upper Tortonian–?Lower Messinian, Mallorca (Spain).

CONCLUSIONS

Our study has shown that:

1. The stratigraphical distribution of *Tarbellastraea* is from the Oligocene (Rupelian) to the Early Messinian. Previously reported pre-Oligocene occurrences of the genus do not belong to *Tarbellastraea*.
2. Of the 25 species and varieties of *Tarbellastraea* previously described, only ten appear to be distinct. Of these ten, two have previously been described only as varieties, and are therefore assigned new names. In addition to these ten, two previously undescribed species have been discovered in the Middle Chattian of the Salento Peninsula of Italy. Thus, a total of 12 species of *Tarbellastraea* appears to have existed in the investigated Mediterranean and European regions during the Oligocene and Miocene.
3. The stratigraphical ranges of nine of the 12 species extend through two or more stages, and they therefore cannot be considered diagnostic of any one stage. However, the two new species from the Salento Peninsula of Italy appear restricted to the Middle Chattian, and *T. ellisiana* is restricted to the Lower Burdigalian of the Aquitaine Basin of France.

4. Although species richness did not change significantly during the evolution of *Tarbellastraea*, overall morphological disparity among species decreased in the genus through time. Early in the evolution of the genus, numbers of septa per corallite ranged from 18–38. Later in its evolution, this range dropped to 24–26. A similar trend can be detected in corallite diameter.
5. Species origination rates appear to have been highest in the genus during the Burdigalian, when high diversity centres may have developed in the Aquitaine basin and Torino regions.
6. Species extinction rates remained relatively constant until the extinction of the entire genus in the latest Miocene. The biggest increase occurred over a relatively short time interval during the latest Tortonian to Messinian, when the genus became extinct and *Porites* dominated the reef-building coral fauna (Esteban, 1979; Pomar, 1991; Riding *et al.* 1991).
7. At the onset of the evolution of *Tarbellastraea*, species had relatively restricted geographical distributions. However, throughout much of the Miocene, all but one species (*T. ellisiana*) were widespread.

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APPENDIX 1

Means (standard deviations) for morphometric species. *, may be biased by preservation.

Character	A (<i>T. tenera</i>)	B (<i>T. distans</i>)	C (<i>T. caryensis</i>)	D (<i>T. raulini</i>)	E (<i>T. ellisiana</i>)
Number of colonies (number of corallites)	10 (150)	8 (78)	18 (107)	16 (148)	20 (188)
NS	24.19 (0.87)	24.42 (1.38)	29.47 (3.66)	23.95 (0.97)	31.46 (3.72)
CD-MIN	1.822 (0.209)	1.866 (0.172)	2.272 (0.328)	2.032 (0.247)	2.144 (0.350)
CD-MAX	2.014 (0.236)	2.044 (0.200)	2.591 (0.375)	2.247 (0.266)	2.388 (0.382)
CD-RAT	0.906 (0.050)	0.915 (0.048)	0.879 (0.062)	0.905 (0.054)	0.888 (0.070)
NND	1.392 (0.424)	2.788 (0.530)	1.304 (0.399)	1.619 (0.490)	1.299 (0.376)
CL1	0.316 (0.090)	0.290 (0.070)	0.322 (0.082)	0.268 (0.095)	0.280 (0.078)
CL2	0.461 (0.102)	0.414 (0.095)	0.477 (0.099)	0.404 (0.108)	0.442 (0.105)
T1	0.546 (0.132)	0.643 (0.150)	0.517 (0.100)	0.555 (0.132)	0.624 (0.148)
T2	0.188 (0.095)	0.134 (0.082)	0.097 (0.066)	0.097 (0.087)	0.094 (0.102)
L1	0.712 (0.084)	0.762 (0.084)	0.980 (0.134)	0.864 (0.112)	0.863 (0.169)
L2	0.570 (0.093)	0.619 (0.106)	0.815 (0.131)	0.696 (0.152)	0.718 (0.178)
L3	0.304 (0.110)	0.325 (0.077)	0.500 (0.129)	0.430 (0.120)	0.452 (0.143)
ST1	0.059 (0.026)	0.045 (0.011)	0.086 (0.034)	0.046 (0.019)	0.063 (0.027)
ST2	0.038 (0.017)	0.030 (0.009)	0.058 (0.024)	0.030 (0.010)	0.042 (0.017)
ST-RAT	0.702 (0.351)	0.689 (0.234)	0.701 (0.235)	0.720 (0.305)	0.712 (0.254)

Character	F (<i>T. chevalieri</i>)	G (<i>T. russoi</i>)	H (<i>T. salentinensis</i>) (<i>T. reussiana</i>)	I (<i>T. reussiana</i>)	J (<i>T. bragai</i>)	Duncan's test results
Number of colonies (number of corallites)	4 (16)	7 (35)	1 (5)	28	4 (24)	—
NS	21.88 (2.96)	33.23 (3.41)	18.40 (3.58)	23.96 (0.89)	24.21 (0.72)	G > E > C > BJAID > F > H
CD-MIN	2.015 (0.390)	2.786 (0.494)	2.160 (0.329)	1.874 (0.201)	2.067 (0.260)	G > CHE $\geq$ JDF $\geq$ IBA
CD-MAX	—	—	—	2.107 (0.229)	2.429 (0.267)	C > JE > D > IBA
CD-RAT	—	—	—	0.891 (0.051)	0.851 (0.055)	BAD $\geq$ IEC > J
NND	0.948 (0.189)	0.575 (0.566)	0.520 (0.205)	1.066 (0.354)	1.974 (0.567)	B > J > DA $\geq$ CE $\geq$ IF > GH
CL1	—	—	—	0.296 (0.076)	0.248 (0.056)	CAI $\geq$ BED $\geq$ J*
CL2	0.402 (0.164)	0.664 (0.263)	0.600 (0.245)	0.453 (0.114)	0.424 (0.072)	G > H > CAIEJBD*F
T1	—	—	—	0.398 (0.073)	0.459 (0.072)	BE > DAC > J > I
T2	0.189 (0.096)	0.091 (0.036)	0.054 (0.013)	0.093 (0.055)	0.141 (0.054)	FA > JBDCEIG $\geq$ H
L1	0.806 (0.144)	1.061 (0.180)	0.780 (0.084)	0.774 (0.105)	—	G > C > DEF $\geq$ HIB $\geq$ A
L2	0.614 (0.136)	0.895 (0.160)	0.600 (0.079)	0.589 (0.133)	—	GC > ED $\geq$ BFGIA
L3	0.187 (0.098)	0.571 (0.184)	0.190 (0.022)	0.348 (0.092)	—	G > CED > IBA > HF
ST1	—	—	—	0.050 (0.017)	0.071 (0.024)	C > J > EA > IDB*
ST2	—	—	—	0.037 (0.011)	0.043 (0.015)	C > JE $\geq$ AI > DB*
ST-RAT	—	—	—	0.762 (0.245)	0.632 (0.177)	I $\geq$ DEACB $\geq$ J*

APPENDIX 2

Means (standard deviations) for primary types in Table 4. *, measured in thin section. **, holotype not seen; measurements after Barta-Calmus (1973).

Code	Species	Number of corallites	NS	CD-MIN	NND
1	<i>abditaxis</i>	7	26.0 (1.9)	1.61 (0.11)	0.56 (0.05)
*2	<i>aquitaniensis</i>	5	23.4 (0.9)	1.622 (0.160)	0.817 (0.119)
3	var. <i>termofuræ</i>	7	24.2 (0.8)	1.41 (0.08)	0.90 (0.10)
*4	<i>carryensis</i>	2	31.0 (7.1)	2.391 (0.369)	1.348 (0.184)
5	var. <i>major</i>	4	36.0 (1.6)	3.29 (0.11)	1.50 (0.29)
6	var. <i>minor</i>	7	24.2 (2.4)	1.76 (0.19)	1.00 (0.35)
7	<i>conoidea</i>	10	25.2 (1.9)	1.93 (0.18)	1.26 (0.27)
**8	<i>distans</i>	—	24 (—)	1.6 (—)	2.9 (—)
9	cf. <i>eggenburgensis</i>	7	26.1 (0.7)	1.80 (0.12)	0.67 (0.16)
10	var. <i>formosa</i>	10	22.5 (2.1)	1.71 (0.18)	0.64 (0.11)
11	var. <i>andalousiensis</i>	7	24.2 (0.8)	1.83 (0.13)	0.83 (0.14)
12	<i>manipulata</i>	10	24.0 (0.0)	2.05 (0.27)	1.19 (0.47)
13	<i>mimbastensis</i>	7	28.7 (3.3)	1.88 (0.23)	0.80 (0.18)
14	<i>prevostina</i>	7	24.0 (0.0)	2.14 (0.10)	1.36 (0.43)
15	<i>profundta</i>	8	38.5 (5.3)	3.46 (0.23)	1.46 (0.53)
16	<i>raulini</i>	7	23.7 (1.2)	1.75 (0.12)	1.58 (0.32)
17	<i>reussiana</i>	10	24.0 (0.9)	2.40 (0.17)	0.80 (0.34)
18	var. <i>echinulata</i>	7	24.2 (0.7)	2.00 (0.10)	1.54 (0.27)
19	<i>siciliae</i>	7	25.2 (1.7)	1.66 (0.14)	1.60 (0.36)
20	<i>tenera</i>	10	24.0 (0.0)	1.71 (0.11)	1.17 (0.23)
21	<i>transsylvanica</i>	10	24.0 (0.0)	2.47 (0.12)	1.29 (0.31)

ARCHITECTURE OF THE UPPER CARBONIFEROUS PTERIDOSPERM FROND *MACRONEUROPTERIS* *MACROPHYLLA*

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ABSTRACT. This paper presents the first full morphological description of *Macroneuropteris macrophylla*, the type species of its genus. The fronds are very similar in size to the more widely distributed *Neuropteris*, but are significantly less divided; the *M. macrophylla* pinnules are homologous to segmented, tertiary pinnae in *Neuropteris*. *M. macrophylla* is known only from westernmost Europe and easternmost North America.

It is now well established that many of the fern-like frond fragments found in the Upper Carboniferous of the palaeoequatorial belt are in fact the remains of seed-bearing plants, sometimes referred to informally as pteridosperms or seed-ferns. Being normally found in a fragmentary condition and without fertile structures, the classification of these fronds has posed serious problems. In recent years, however, attempts have been made to produce a more natural classification by using details of the frond architecture (i.e. the pattern of branching within the frond) and, more recently, epidermal structure.

The genus *Macroneuropteris* was erected by Cleal *et al.* (1990) as part of a taxonomic revision of one of these groups of pteridosperm fronds, previously assigned to *Neuropteris* (Brongniart) Sternberg. Laveine (1967, p. 80) had noted earlier that some species of *Neuropteris sensu lato* have less divided fronds and larger pinnules, referring to the group as the *Neuropteris* 'macrophylliens'. Laveine (1967, p. 314) maintained that these differences in frond architecture could largely justify the creation of a new genus, but was reluctant to make a formal taxonomic change, because of the possible disadvantages of splitting an apparently continuous evolutionary lineage. However, this stance was based exclusively on gross morphology. The cuticular evidence, such as that presented by Barthel (1961) and Cleal and Zodrow (1989), added weight to the argument for the generic separation of *Macroneuropteris*. The gross morphology nevertheless remains a key feature for understanding these fronds, and this has never previously been the subject of a detailed published investigation. The present paper therefore presents the first detailed description of the frond architecture of the type species, *Macroneuropteris macrophylla* (Brongniart) Cleal, Shute and Zodrow.

MATERIALS AND METHODS

The description is based on eight specimens in the palaeontological collections of The Natural History Museum, London, accession numbers V.3073 and V.63414–V.63419. Their provenance is stated as 'Coal Measures, Radstock, Somerset'. They probably originated from the Radstock Formation, and are thus late Westphalian D in age (*Dicksonites plueckenetii* Subzone *sensu* Cleal 1991; Cleal and Thomas 1994). All but V.63419 are stated to have been presented to the museum in the 1880s by Mr J. McMurtrie, a nineteenth-century geologist well known for his work on this coalfield (e.g. McMurtrie 1867, 1890, 1901). One of the specimens (V.63417) has been previously figured by Crookall (1959, pl. 42, fig. 3).

The specimens required no preparation, and were photographed using plane- or cross-polar illumination. Outline tracings were taken from the photographs, and then rescaled to a uniform magnification. These tracings are the basis of Text-figures 1–2. Plant macrofossils from the Bristol–Somerset Coalfield are unsuitable for cuticle work, but the epidermal structures of this species have been described previously by Cleal and Zodrow (1989), based on Canadian material.

The cuticular evidence described in these studies has been annexed to the emended diagnoses given in the systematic palaeontology section below.

Terminology for frond architecture follows that used by Cleal and Shute (1991). For the sake of simplicity, the terms 'upper' and 'lower' have been used instead of 'distal' and 'proximal' in the descriptions when referring to position in a frond segment. The term pinnule is used in its now widely accepted sense (e.g. Tryon 1960; Taylor and Taylor 1993; Niklas 1993) for the ultimate segment of the frond, irrespective of the order that the segment is within the frond.

DESCRIPTION

The specimens dealt with in this study fall into three broad groups: (1) wide rachises with broad, ovoid pinnules attached (V.63416(b), V.3073); (2) wide, dichotomous rachises (V.63416(a) and possibly V.63418); and (3) pinnate foliage with mainly elongate, linguaeform to subfalcate pinnules (V.63414, V.63415, V.63417, V.63419). These are taken to be the lower, middle and upper regions, respectively, of a bipartite frond. Some of the dimensions of these specimens are summarized in Table 1.

TABLE 1. Main dimensions of *Macroneuropteris macrophylla* frond fragments (in mm).

Specimen no.	Primary width	Maximum primary rachis branch width	Secondary rachis spacing (outer/inner) ¹	Secondary rachis offset ²	Maximum pinnule length
V.63417	—	10	90/90	50	45
V.63415	—	10	—/—	—	45
V.63419(b)	—	9	90/—	—	60
V.63418	—	8	90/90	70	45
V.63414	—	8	90/100	50	50
V.63416(b)	16	—	—/—	—	—
V.63419(a)	—	4	100/—	—	55
V.63416(a)	7	4	40/40	21	22
V.3073	9	—	—/—	—	—

All measurements in millimetres.

¹ Refers to spacing on the outward and inward facing sides of the primary rachis branch.

² Refers to the distance between a secondary rachis on the outward facing side of the primary rachis branch, and the next, higher secondary rachis on the inward facing side of the primary rachis branch.

As these specimens were collected over 100 years ago, it is impossible to place the fossils in any sedimentological context, other than to state that they are preserved in a mudstone, possibly representing a flood-basin deposit.

Lower part of frond

The lowest preserved part of the frond is shown in V.3073 and V.63416(b) (Pl. 1; Pl. 2, fig. 3; Text-fig. 1C–D). Primary rachises, up to 190 mm long and 7–9 mm wide, have large pinnules alternately

EXPLANATION OF PLATE I

Macroneuropteris macrophylla (Brongniart) Cleal *et al.* V.63416; two frond fragments, one of a primary rachis below the main dichotomy of the frond, the other of the main dichotomy; photographed using cross-polarized reflected light; Radstock, Somerset, UK; upper Westphalian D; $\times 1$.



or sub-oppositely arranged. Pinnule spacing on either side of the rachises is 25–33 mm, and the ratio of pinnule spacing to rachis width is *c.* 2.5. Neither specimen shows the primary rachis attached to a cauline axis.

This part of the frond is also shown by the specimen figured by Kidston (1888, pl. 21, fig. 2). This shows a 135 mm length of primary rachis which is only 5 mm wide. The attached pinnules are arranged oppositely along the rachis at intervals of 15–16 mm; the ratio of pinnule spacing to rachis width is thus slightly higher (3.0–3.2) than in the specimens figured here.

Dichotomy of primary rachis

At least 190 mm from the point of attachment to the stem, the primary rachis underwent a dichotomy to produce two primary rachis branches. This dichotomy is clearly seen in V.63416(a) (Pl. 1; Text-fig. 1B). From the dimensions of the rachises and of the attached pinnules, it is apparent that V.63416(a) was part of a much smaller frond than that represented by most of the other specimens dealt with in this study. Such a small frond may have originated from near the top of a plant, or is perhaps the leaf of a small, juvenile plant. Whichever is correct, there is no reason to believe that the architecture of this small frond was significantly different from that of the larger fronds.

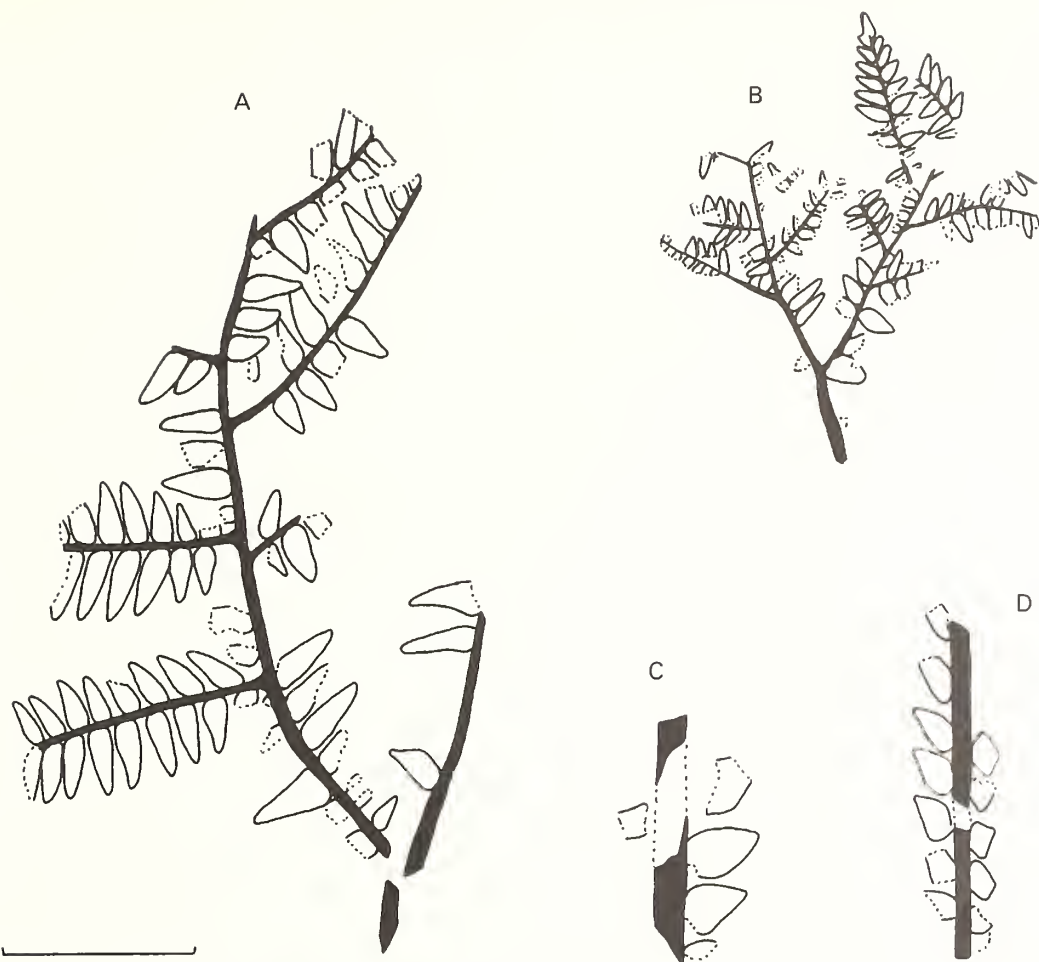
In V.63416(a), the primary rachis branches lie at 45° to one another, but there was probably some taphonomic distortion and this angle may have been wider in life. This distortion is most clearly seen in the left-hand primary rachis branch. If the angle between the primary rachis and the right-hand branch is about what it was in life, then the angle of the main frond dichotomy would be *c.* 70°. A narrower angle would cause the secondary rachises to overlap significantly in the middle of the frond, reducing the photosynthetic efficiency of the frond, and thus seems a less likely configuration. A similar situation arises with the specimen figured by Kidston (1888, pl. 21, fig. 2); the primary rachis branches are preserved at an angle of about 40° to one another, but in this case the right-hand branch has clearly been bent towards the centre of the frond. If the left-hand branch is taken to provide a better indication of the angle, then a value of about 65° is obtained for this dichotomy.

A similar angle of dichotomy of about 70° may occur in *Macroneuropteris scheuchzeri* (Laveine and Brousmiche 1982), as well as in other bipartite trigonocarpalean (medullosan) fronds (e.g. *Neuropteris*, *Odontopteris*, *Callipteridium* and *Margaritopteris*; Zeiller 1900; Potonié 1903; Laveine *et al.* 1977; Wendel 1980; Zedrow and Cleal 1988; Cleal and Shute 1991). One specimen (V.63418; Text-fig. 1A) appears to show a somewhat narrower angle of 55–60°, but there is again clearly some taphonomic distortion here. Nevertheless, some variation in the angle of the main dichotomy has been reported in certain other genera, such as *Cardioneuropteris* (Goganova *et al.* 1993) and *Eusphenopteris* (Laveine 1993), and the same may also have occurred in *M. macrophylla*.

Primary rachis branches

The longest preserved fragment is 380 mm long (V.63417; Pl. 2, fig. 1; Text-fig. 2A), but is clearly incomplete. The width of the main rachis of the branch is 10 mm at the base and tapers distally to 2 mm. Although the upper part of this specimen has been subject to some taphonomic distortion, it is likely that the pinna fragment with the apical pinnule preserved represents the apex of the primary rachis branch. The primary rachis branch widths of all the other specimens investigated in this study fall within this range, except for specimen V.63415 which is 11 mm wide at its broken lower part.

The lowest part of the primary rachis branch in V.63417 appears straight, but becomes kinked where each secondary rachis is attached higher in the frond. Most of the other specimens show similar kinking of the primary rachis branches. About half-way along the V.63417 primary rachis branch, there is what appears superficially to be a pseudodichotomy of the primary rachis branch,



TEXT-FIG. 1. *Macroneuropteris macrophylla* (Brongniart) Cleal *et al.* Lower parts of frond; Radstock, Somerset, UK; upper Westphalian D. A, V.63418; possible main dichotomy of frond, although the two branches are not preserved attached. B, V.63416(a); main dichotomy of small frond, reconstructed from a bent frond fragment that lies on either side of the rock slab. C, V.63416(b); primary rachis below main dichotomy with large pinnules attached. D, V.3073; primary rachis below main dichotomy with large pinnules attached. Scale bar represents 100 mm.

but this is probably the result of taphonomic distortion (note the displacement of the secondary rachises in the upper part of this specimen). A possible overtopped branch or even dichotomy of the primary rachis branch is shown in one of the fragments on V.63419 (Pl. 3, fig. 2; Text-fig. 2B), but again it is not well enough preserved to be sure if it was an original feature (other previously published examples of such branching are by Lesquereux 1879, pl. 9, fig. 2; Kidston 1888, pl. 22, fig. 2; and Crookall 1959, pl. 40, fig. 1).

V.63416(a) (Pl. 1; Text-fig. 1B) shows that the secondary rachises are attached to the two primary rachis branches of a frond at the same distance from the main dichotomy. Consequently, the inwards facing secondary rachis tips must have met more or less in the middle of the frond. There is no evidence as to whether this arrangement persisted in the higher parts of the frond.

There is little direct evidence as to the shape of the two frond segments produced by the dichotomy of the primary rachis. Very few complete secondary rachises/pinnae have been found

attached to the primary rachis branches. Although V.63417 shows the upper end of a primary rachis branch, it is impossible from this alone to determine the form of the apex of the frond segments.

Secondary rachises

Secondary rachises are attached alternately to the primary rachis branches. The lowest secondary rachises are emitted from the outwards facing sides of the primary rachis branches. In V.63416(a) (Pl. 1; Text-fig. 1B), the lowest secondary is *c.* 60 mm above the dichotomy, although this distance was probably greater in the larger, more 'typical' fronds. The angle of attachment of the secondary rachises to the primary rachis branches appears to have been 80–90° in much of the frond, although towards the frond apex the angle became narrower: 60° in V.63414 (Pl. 3, fig. 1; Text-fig. 2D) and 53° in the specimen figured by Crookall (1959, pl. 40, fig. 1). An even more acute angle is suggested by V.63417 (Pl. 2, fig. 1; Text-fig. 2A), although this may be due to taphonomic distortion.

As mentioned above, very few complete secondary pinnae have been found attached to the primary rachis branches, the only exceptions being in V.63416(a), V.63417 and V.63419(b) (Pl. 1; Pl. 2, figs 1–2; Text-figs 1B, 2A, C). From the evidence provided by the available fragments, however, they appear to have been parallel-sided for most of their length, tapering only slightly near their position of attachment to the primary rachis branch. More marked tapering occurs in the apical part of the secondary rachises, which are terminated by a single rhomboidal apical pinnule, thus exhibiting clearly an imparipinnate configuration. The terminal pinnule often shows a lateral lobe which demonstrates the mode of differentiation of the lateral pinnules from the terminal. The longest preserved secondary rachis fragment is 250 mm long (V.63419(b); Text-fig. 2C) and, from the way the attached pinnules taper in the upper part of the fragment, was probably originally *c.* 300 mm long.

Pinnules

These are found attached to all orders of rachis, both above and below the main dichotomy. The range of pinnule morphology seen in the frond is shown in Plate 4.

The most commonly found pinnule forms of this species occur along the secondary rachises (Pl. 4, figs 1–2). They are linguaeform, subfalcate or subtriangular in shape, up to 55 mm long and 15 mm wide. They are constricted, often somewhat cordate, at the base. There is usually a distinct, subauriculate basiscopic expansion, while the lamina on the acroscopic side is markedly constricted. This gives the basal part of the pinnules a distinctly asymmetrical, decurrent appearance. The pinnules have a generally acute or sometimes obtuse apex.

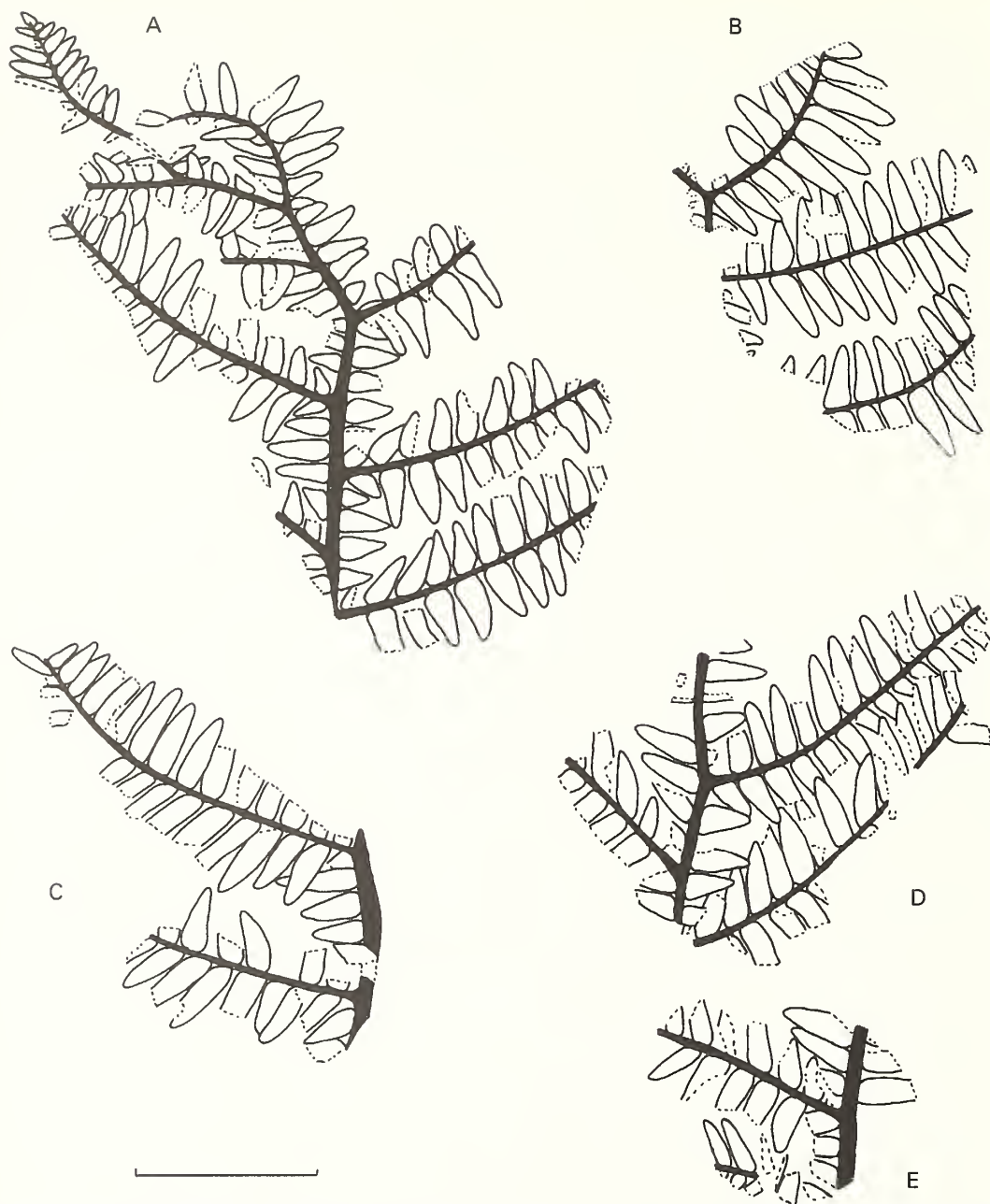
Three or four pinnules are intercalated between adjacent secondary rachises on the primary rachis branches (Pl. 4, fig. 3). They are rather similar in shape to the 'typical' pinnules described in the previous paragraph. However, the acroscopic constriction tends to be less marked in the intercalated pinnules and, in some cases, there may even be an acroscopic bulge. Moreover, adjacent to the secondary rachises, where the space available for growth is more limited, they are often squatter and more subtriangular.

V.63416(a) (Pl. 1; Pl. 4, fig. 4; Text-fig. 1B) shows that immediately below the lowest of the secondary rachises, the pinnules attached to the primary rachis branches are similar to the 'typical'

EXPLANATION OF PLATE 2

Figs 1–3. *Macroneuropteris macrophylla* (Brongniart) Cleal *et al.* Specimens photographed using cross-polarized reflected light; Radstock, Somerset, UK; upper Westphalian D. 1, V.63417; near-terminal fragment of primary rachis branch; $\times 0.5$. 2, V.63416; pinna terminal from obverse side of specimen shown in Plate 1, representing continuation of the distal-most preserved inside pinna from the right-hand primary rachis branch; $\times 1$. 3, V.3073; primary rachis below main dichotomy of frond with swollen pinnules; $\times 0.5$.





TEXT-FIG. 2. *Macroneuropteris macrophylla* (Brongniart) Cleal *et al.* Upper parts of frond, A and B showing possible pseudodichotomies; Radstock, Somerset, UK; upper Westphalian D. A, V.63417. B, V.63419(a). C, V.63419(b). D, V.63414. E, V.63415. Scale bar represents 100 mm.

pinnules attached to the secondary rachises. Approaching the main dichotomy of the frond, however, the pinnules become broader, with a subtriangular or ovoid shape. V.63416(b) and V.3073 (Pl. 1; Pl. 2, fig. 3; Text-fig. 1C–D) show that the pinnules below the main dichotomy are consistently broader and more ovoid, achieving dimensions of up to 50 mm long and 30 mm wide. There is

therefore a gradual transition between the large, ovoid pinnules attached to the primary rachis below the main dichotomy, and the more 'typical' elongate linguaeform to subfalcate intercalated pinnules higher in the frond. From this, it seems reasonable to assume that the large pinnules in the lower part of the frond lay in the same plane as the 'typical' pinnules above the main dichotomy.

The large pinnules near the base of the frond have fine, dichotomous veins radiating from their point of attachment to the rachis (Pl. 4, fig. 4). In the more elongate forms, however, there is a thick midvein along the long axis of the pinnule (Pl. 4, figs 1–2). The midvein is virtually non-decurrent in most pinnules and extends for some 90 per cent. of their length. Pinnules near the apex of the secondary rachises may have a somewhat decurrent midvein, which extends only for some of the pinnule length. Lateral veins are emitted from the midvein at a very narrow angle, and then arch broadly to meet the pinnule margin at about right-angles. The veins dichotomize three to five times, to produce a nervation density of *c.* 45 veins per 10 mm along the pinnule margin.

In no case was any evidence found of lobed (except for some terminals) or pinnatifid pinnules, forming a transition to divided pinnae. Each half of the frond produced by the major dichotomy of the primary rachis was thus essentially bipinnate.

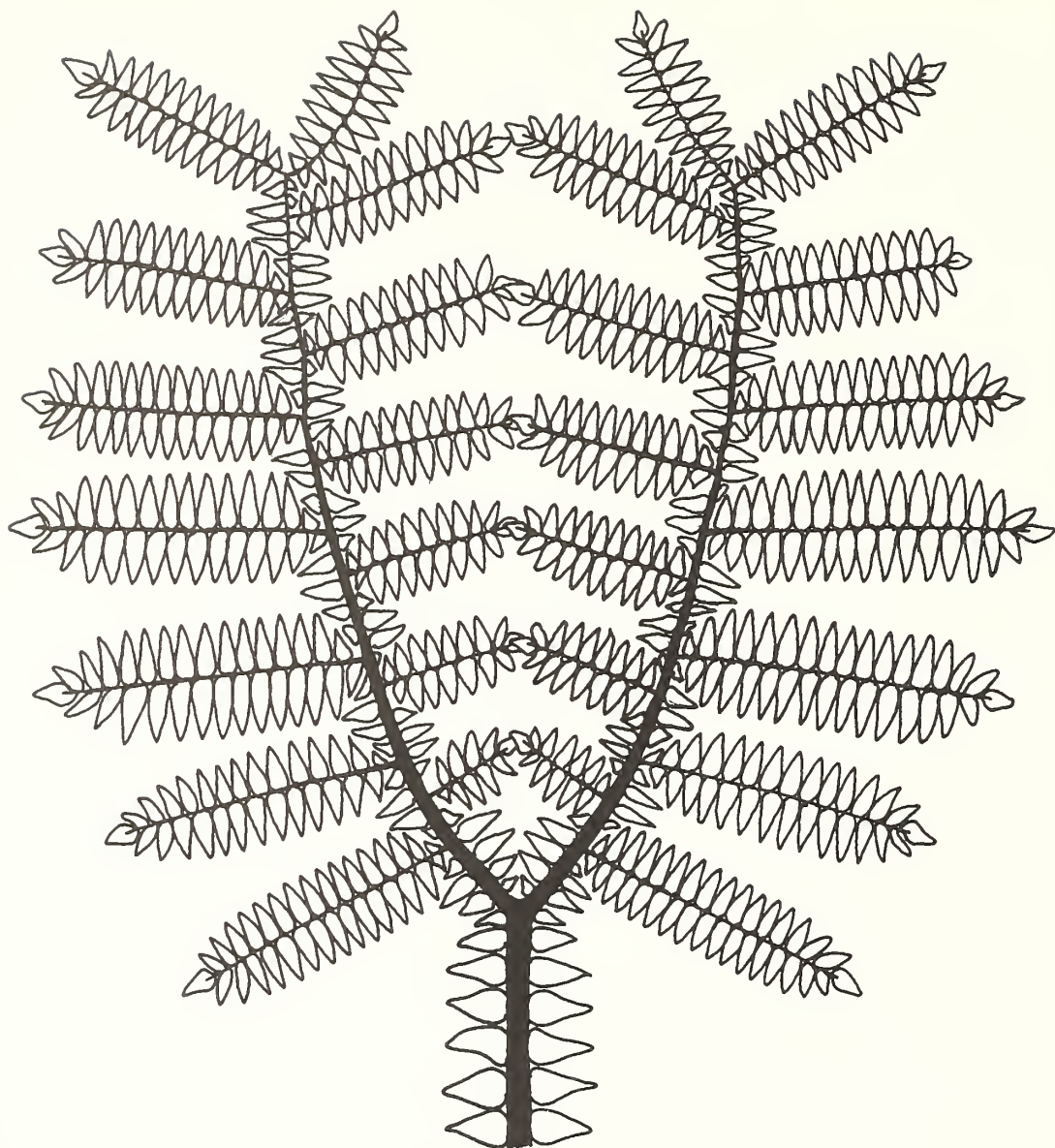
INTERPRETATION OF FROND

Our interpretation of the *Macroneuropteris macrophylla* frond is summarized in Text-figure 3. The main features of the reconstruction are fairly self-evident from the specimens: (1) an essentially bipartite architecture; (2) large, pyriform pinnules attached to the primary rachis below the main dichotomy, and more or less orientated in the same plane as the rest of the frond; (3) bipinnate primary rachis branches; (4) intercalated pinnules between the secondary rachises; and (5) pinnae terminated by single apical pinnules.

The two available specimens of *M. macrophylla* showing the main dichotomy of the frond (Pl. 1; Text-fig. 1B; Kidston 1888, pl. 21, fig. 2) show that there is a morphological gradation between the large, pyriform pinnules and the normal-shaped intercalated pinnules attached to the primary rachis branches. There is thus some comparison with the model proposed by Laveine (1967, p. 81), whereby the cyclopterid pinnules attached to the lower part of the fronds in some *Neuropteris* species (subsequently transferred to *Laveineopteris* by Cleal *et al.* 1990) also graded morphologically into normal-shaped pinnules. In contrast, using a combination of evidence from gross morphology and cuticles, Cleal *et al.* (1990) have argued that these cyclopterids of *Laveineopteris* foliage were of a fundamentally different nature to the pinnate foliage from higher in the fronds (a point of view which had also been earlier partly expressed by Potonié 1903). The status of these cyclopterids attached to *Laveineopteris* fronds remains a subject of contention, and the present authors must confess to being in some disagreement on the matter. However, they do agree that the large, pyriform pinnules of the *M. macrophylla* fronds are *not* fundamentally different from the pinnate foliage from higher in the frond, in either a functional or morphological sense.

The symmetry of the frond, with the secondary pinna tips meeting in the middle, may seem unlikely, since it results in gaps in the lamina cover in the middle of the frond; a more complete lamina cover would have resulted if the two sets of secondary pinnae were offset. We have reconstructed it in this way based on the position of attachment of the secondary rachises observed immediately above the main dichotomy. However, we recognize that there is no direct evidence of this higher in the frond, and it will have to be confirmed by more complete specimens. It is even likely that there was a probable large variation in this point.

Except for V.63416(a) and V.3073 (Pl. 1; Pl. 2, fig. 3; Text-fig. 1B, D), the dimensions of the frond fragments studied here show a remarkable consistency (see Table 1). For instance, the maximum width of the primary rachis branches in each specimen is 8–11 mm, and the secondary rachises are spaced at 90–100 mm. From this, it is assumed that most of these fragments originated from fronds of about the same size. The reconstruction that we present here is the smallest and thus simplest that can accommodate all of the available specimens, and results in a frond that is *c.* 0.8 m long from the main dichotomy to the apex (the so-called DAD dimension of Cleal and Shute 1991). Clearly,



TEXT-FIG. 3. Proposed reconstruction of an entire frond of *Macroneuropteris macrophylla* (Brongniart) Cleal *et al.* This frond would be about 1 m long.

a longer frond could be proposed, simply by extending the petiole and the primary rachis branches, and adding more secondary rachises. However, it would be expected that this would result in primary rachis branches that were wider near the main frond dichotomy.

V.63416(a) and V.3073 are smaller in most of their dimensions than the other specimens. If there is a broad correlation between these dimensions and the overall frond length, then these specimens probably originated from fronds only about half as long (DAD 0.40–0.45 m).

In the absence of more complete specimens, the overall width of the fronds is also difficult to assess. It depends mainly on the angle of the main dichotomy of the frond and the length of the

outwards-facing secondary rachises, the latter variable being unknown. The longest secondary rachis in our specimens appears to have been originally *c.* 0.3 m long, although it is not completely preserved (V.63414). By incorporating a secondary rachis of this length into our reconstruction, the frond width comes to something of the order of 1 m.

SYSTEMATIC PALAEOONTOLOGY

The suprageneric taxonomy used in this paper follows that of Meyen (1984, 1987). In particular, the original name *Trigonocarpales* is adopted in preference to the more widely used *Medullosales*, as it is linked to a form-genus of a fructification rather than of a stem. However, as there is no direct evidence of the fructifications of *Macroneuropteris*, the latter is assigned to the order as a satellite form-genus (*sensu* Meyen 1978; Thomas and Brack-Hanes 1984).

The following annotations are used in the synonymy lists following Matthews (1973), Zodrow and Cleal (1993), and Cleal and Shute (1995).

* The protologue of the basionym.

§ The valid publication of the name accepted here.

T The type specimen(s) when not published in the protologue, or photographic illustrations of them if the original illustrations were poor.

? The inclusion of this reference is provisional due, for instance, to poor illustration.

. The present authors accept responsibility for including this in the synonymy; if a species is included as a synonym without the '·', then it is based on another authority, which is quoted at the end of the reference.

† (Dagger-sign) for the most recent reference which includes a reasonably full synonymy and extensive illustration.

k The reference includes cuticular evidence.

f The reference includes frond architecture evidence.

Division GYMNOSPERMOPHYTA

Order TRIGONOCARPALES Seward, 1917, *emend.* Meyen, 1984

Satellite form-genus MACRONEUROPTERIS Cleal, Shute and Zodrow, 1990

Type. Holotype of *Macroneuropteris macrophylla* (Brongniart) Cleal, Shute and Zodrow, 1990 by original designation.

Macroneuropteris macrophylla (Brongniart) Cleal, Shute and Zodrow, 1990

Plates 1–4; Text-figures 1–3, 5

- *1831 *Nevropteris macrophylla* Brongniart, p. 235, pl. 65, fig. 1.
- ?1831 *Nevropteris acutifolia* Brongniart, p. 231, pl. 64, figs 7 [photographically refigured by Laveine 1967, pl. F, fig. 1], ?6.
- 1858 *Neuropteris Clarksoni* Lesquereux, p. 857, pl. 6, figs 1–4 [*vide* Kidston 1888].
- f1888 *Neuropteris macrophylla* Brongniart; Kidston, p. 354, pl. 21, fig. 2; pl. 22, fig. 2 (*non* fig. 3 [= *Neuropteris flexuosa* Sternberg]).
- ?1940 *Neuropteris Machadicostai* Teixeira, p. 91, pls 3–4.
- f†T1959 *Neuropteris macrophylla* Brongniart; Crookall, p. 176, pl. 38, fig. 4; pl. 39, fig. 1; pl. 40, figs 1–2 [photographic copy of Kidston 1888, pl. 22, fig. 2]; pl. 42, figs 1, 3 (*non* pl. 40, fig. 3 [copy of Kidston 1888, pl. 22, fig. 3 = *Neuropteris flexuosa* Sternberg]).
- k1989 *Neuropteris macrophylla* Brongniart; Cleal and Zodrow, p. 860, pls 104–105.
- §1990 *Macroneuropteris macrophylla* (Brongniart) Cleal *et al.*, p. 488.

Type. Holotype, by original designation, is Specimen No. 5151 of the Geological Society Collection, British Geological Survey, Keyworth, Great Britain. Provenance: Radstock Formation (upper Westphalian D), Dunkerton, near Radstock, Somerset.

Emended diagnosis. Bipartite frond, typically *c.* 1 metre long. Main dichotomy at least 190 mm from base of frond, at an angle of 65–70°, producing two bipinnate frond segments. Primary rachis

branches with a slight inward curve in their proximal part. Secondary rachises attached alternately to primary rachis branches at 80–90°. Secondary pinnae parallel-sided for most of length, tapering at their distal end and to a lesser extent in their proximal part. Pinnae terminated by a single, rhomboidal apical pinnule. Pinnules attached laterally to both primary and secondary rachises, and intercalated between secondary pinnae on primary rachis branches, and all lie in the same plane within frond. Above main frond dichotomy, pinnules typically linguaeform to subfalcate, up to 55 mm long and 15 mm wide, with more or less acute apex. Base of pinnules asymmetrically cordate, with significantly more prominent lobe on basiscopic side. Near junctions of rachises, pinnules become squatter and more subtriangular. Below main dichotomy of frond, pinnules are ovoid, up to 50 mm long and 30 mm wide. The broader, ovoid pinnules near base of frond have fine, radiating veins. In other pinnules, there is a prominent midvein, extending for much of pinnule length. Broadly arching lateral veins meet pinnule margin at about right-angles; they fork three to five times, producing nervation density of *c.* 45 veins per 10 mm on pinnule margin.

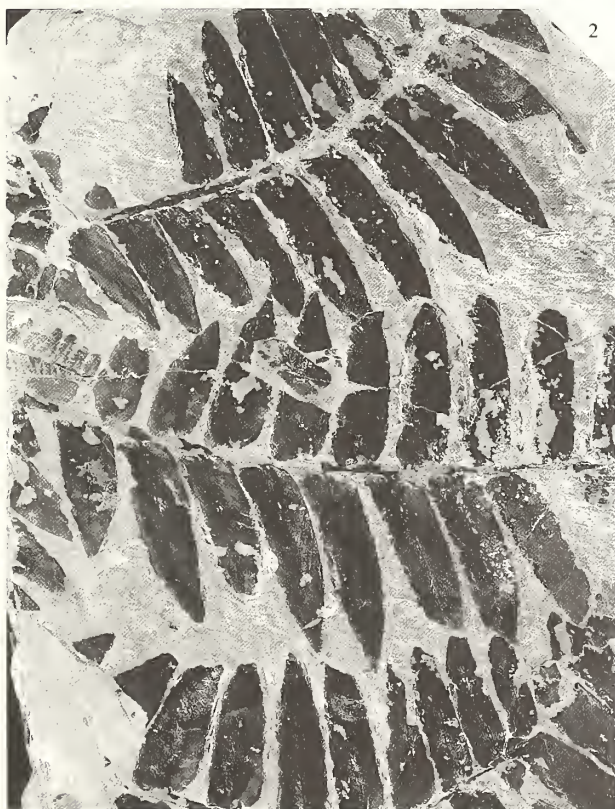
Pinnule epidermis hypostomatic; stomata brachyparacytic, with raised subsidiary cells, and polar axis orientated parallel to veins. Guard cells 20–25 μm long. Stomatal index 9–11. Adaxial epidermal cells uniformly isodiametric, up to 60 μm in size, except along midvein where they are elongate, up to 160 μm long and 50 μm wide. Abaxial epidermal cells papillate. Intercostal abaxial cells irregularly polygonal, up to 60 μm in size; costal abaxial cells more elongately subrectangular, up to 140 μm long and 30 μm wide. Multicellular file trichomes, up to 30 μm wide (length unknown), uniformly distributed over abaxial surface; none present on adaxial surface.

Comparisons and remarks on synonymy. The principal taxonomic problem concerns the synonymy with *Neuropteris clarksonii* Lesquereux, the type of which originated from Oliphant, in the Northern Anthracite Coalfield of Pennsylvania. That the two species are identical has been accepted by most European authors, on the authority of Kidston (1888), although some American palaeontologists continued to use Lesquereux's later name (e.g. Noe 1925). Bell (1938) suggested that Lesquereux's species might be given priority, due to the inadequacy of Brongniart's illustration, but this argument (doubtful anyway on strict nomenclatural grounds) is no longer acceptable following Crookall's photographic illustration of the *M. macrophylla* holotype. We accept unequivocally the synonymy of the two species. To support our view we illustrate (Pl. 3, fig. 3) a specimen from the Appalachian Coalfield, which was identified as *N. clarksonii* by a leading nineteenth-century North American palaeobotanist, R. D. Lacoe, and which agrees in all features with *M. macrophylla*.

Brongniart (1831) figured some poorly preserved specimens from the Somerset Coalfield ('near Bath') under the name *N. acutifolia*. This has been widely regarded as a later synonym of *Macroneuropteris scheuchzeri*, mainly following Bunbury (1847). Laveine (1967, pl. F, fig. 1) illustrated photographically one of Brongniart's types (his fig. 7, the specimen shown on fig. 6 cannot currently be found), and shows that it has a subtriangular pinnule with a marked subauriculate basiscopic expansion. Pinnules of this shape and with a basiscopic lobe are found very commonly in *M. macrophylla* fronds (e.g. Crookall 1959, pl. 39, fig. 1; pl. 40, fig. 1), although they also sometimes occur in *M. scheuchzeri* (e.g. Bertrand 1930, pl. 11, fig. 2). The surface of the pinnule shows one or two doubtful lines, which might be the remains of epidermal trichomes, but the

EXPLANATION OF PLATE 3

Figs 1–3. *Macroneuropteris macrophylla* (Brongniart) Cleal *et al.* 1–2, specimens photographed using cross-polarized reflected light; Radstock, Somerset, UK; upper Westphalian D. 1, V.63414; middle part of primary rachis branch showing clear development of intercalated pinnules. 2, V.63419(a); near-terminal fragment of primary rachis branch showing possible pseudodichotomy. 3, V.1976; specimen coated with ammonium chloride and photographed using plain light; Cannelton, Beaver County, north-western Pennsylvania, USA; Kittanning Coals, Allegheny Series (= Westphalian D); ultimate pinna terminal, typical of that identified by North America palaeobotanists as *Neuropteris clarksonii* Lesquereux. All $\times 0.5$.



evidence is equivocal. The evidence tends to suggest that Brongniart's figure 7 belongs to *M. macrophylla*, although one of us (JPL) has examined other, unillustrated material identified by Brongniart as *N. acutifolia*, which undoubtedly belongs to *M. scheuchzeri*.

Very similar material, from the Westphalian D of the Santa Sousa Basin in southern Portugal, was described under the name *Neuropteris machadicostae* Teixeira, 1940. Many of the specimens have large, asymmetrical pinnules with a conspicuous, subauriculate basiscopic expansion, and are almost identical to the pinnules attached to the secondary rachises of *M. macrophylla* (Pl. 4, figs 1–2). They are associated with subtriangular pinnules (Teixeira 1940, pl. 4, figs 3, 5) that can be compared directly to the shorter intercalated pinnules in *M. macrophylla* (Pl. 4, fig. 3). There is even one example of a pyriform pinnule (Teixeira 1940, pl. 3, fig. 7) that looks identical in shape to the large pinnules from below the main dichotomy of the *M. macrophylla* frond (Pl. 4, fig. 4). Teixeira regarded his material as having more elongate pinnules than *M. macrophylla*. However, this was probably because he took a specimen figured by Seward (1910, p. 569), which in fact is quite atypical in morphology, as a typical representative of the latter species. When compared with the specimens documented in the present paper, there can be seen to be little justification in not assigning these Portuguese specimens to *M. macrophylla*.

Crookall (1959) regarded *Neuropteris squarrosa* Ettingshausen, 1852, from the middle Westphalian of Czechoslovakia, as a later synonym of *M. macrophylla*. However, Němejc and Šetlík (1950) had earlier noted that the former had anastomosed veins, and referred the specimens to *Linopteris neuropteroides* (Gutbier).

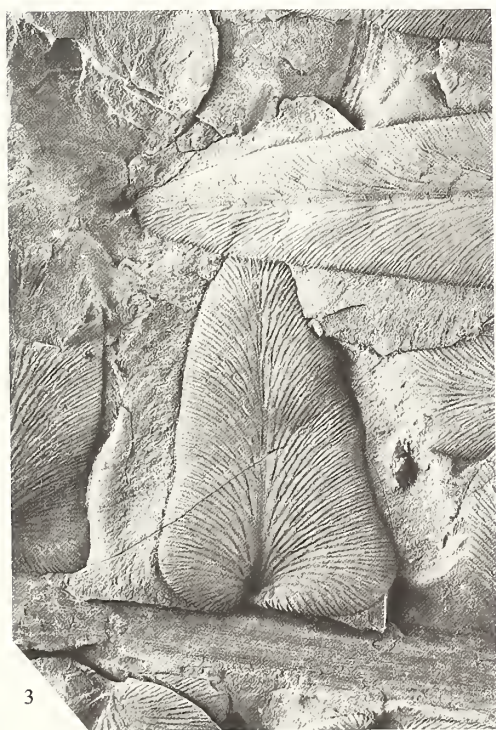
General remarks. There is no direct evidence of the fructifications or cauline anatomy of this species. Lesquereux (1880) comments that his specimens were associated with seeds 'typical of *Neuropteris*', but he does not describe or illustrate them. The species is included within the Trigonocarpaceae (Medullosales auctt.) based on the broad similarity of its frond architecture with *Neuropteris ovata* Hoffmann, which has been demonstrated to be attached to *Medullosa noei* Steidtmann axes (Beeler 1983).

Distribution. The best illustrated records of *M. macrophylla* from Europe are from the Radstock and Farrington formations, in the Bristol–Somerset Coalfield (Kidston 1888; Moore 1938; Crookall 1959). There is also unpublished evidence from the Publow Formation of the same coalfield (R. H. Wagner, pers. comm.). The only other reliable record from Europe is from the Westphalian D of the Santa Sousa Basin of Portugal. Records from the Bolsovian and Duckmantian of Britain mentioned by Crookall (1959) cannot be substantiated and probably represent misidentifications of *Macroneuropteris scheuchzeri*. The records listed by Crookall from elsewhere in Europe are over a century old and unillustrated, and must be treated with considerable suspicion.

The best documented records from North America are from the Maritime Provinces of Canada, where it has been found associated with the Harbour, Lloyd Cove and Point Aconi seams (upper Morien Group; upper Westphalian D to lower Cantabrian) of the Sydney Coalfield (Bell 1938; Zodrow 1986; Cleal and Zodrow 1989). In the rest of North America, there are well-documented records from the Northern Anthracite Coalfield, near Wilkes-Barre in north-east Pennsylvania (Lesquereux 1854, 1879, 1880). Few stratigraphical details were supplied, but the specimens probably originated from the upper Allegheny (Darrah 1969), and are thus probably of late Westphalian D or early Cantabrian age (Wagner in press). Lesquereux (1880) also described specimens from the Kittanning Coals worked at Cannelton, in the northern part of the Appalachian Coalfield. These, again, are likely to be late Westphalian D in age, although perhaps marginally older than the

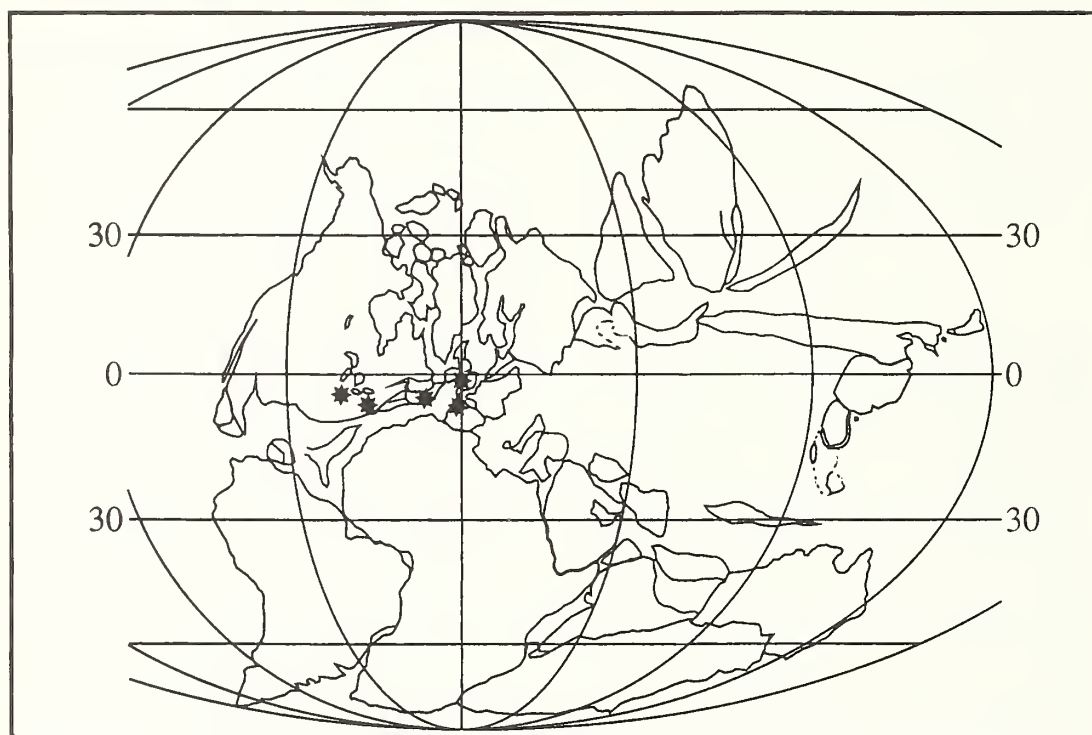
EXPLANATION OF PLATE 4

Figs 1–4. *Macroneuropteris macrophylla* (Brongniart) Cleal *et al.* Range of morphology in pinnules, photographed under ammonium chloride; Radstock, Somerset, UK; upper Westphalian D. 1, lanceolate lateral pinnule attached to secondary rachis. 2, subfalcate lateral pinnule attached to secondary rachis. 3, subtriangular, intercalated pinnule attached to primary rachis branch. 4, swollen pinnule attached to primary rachis, below main dichotomy of frond. 1–3, V.63414; 4, V.63416(b). All $\times 2$.





TEXT-FIG. 4. *Macroneuropteris scheuchzeri* (Hoffmann) Cleal *et al.* V.63894; close-up of typical pinnules showing epidermal hairs, photographed under plane-polarized light; Radstock, Somerset, UK; upper Westphalian D; $\times 2$.



TEXT-FIG. 5. Geographical distribution of *Macroneuropteris macrophylla* (Brongniart) Cleal *et al.*, plotted on a Late Carboniferous base map from Thomas and Cleal (1993, p. 5), originally adapted from Laveine *et al.* (1993).

specimens from the Northern Anthracite Coalfield (Darrah 1969; Pfefferkorn and Gillespie 1980). White (1900) gave an unillustrated record of this species from the Southern Anthracite Coalfield of Pennsylvania, from strata equivalent to or marginally older than the Cannelton occurrences.

Darrah (1969) argued that records of this species from Mazon Creek in fact refer to *Neuropteris decipiens* Lesquereux. The latter is an equivocal species, very similar to *Macroneuropteris scheuchzeri* except in the apparently larger size of the pinnules.

From outside of the eastern belt of US coalfields, there are records of this species from the Western Interior Coalfield of Missouri (White 1893) and Kansas (Sellards 1908; Cridland *et al.* 1963). Sellards' specimens originated from the Canabiss Formation, and are approximately coeval with the Wilkes-Barre material, but Cridland *et al.* dismissed them as misidentified specimens of *Macroneuropteris scheuchzeri*. The material identified by Cridland *et al.* as *N. clarksonii* (i.e. *M. macrophylla*) originated from a higher stratigraphical horizon, in the Missourian (?Stephanian B). The specimens have subtriangular pinnules with a narrowly acute apex, and many show a clear proximal curvature. They are thus quite different from the typical form of *M. macrophylla* and are more similar to the specimens figured by Cridland *et al.* as *Neuropteris hastata* White.

M. macrophylla thus appears to be restricted to a narrow area of westernmost Europe and eastern North America, which in most Late Carboniferous palaeogeographies are shown to be close together (Text-fig. 5). However, this restricted distribution may also reflect stratigraphical factors. The Somerset Coalfield is one of the few northern European paralic coalfields to range up into the upper Westphalian D and it is possible that the *M. macrophylla*-bearing plant existed in some other paralic coal basins, whose sequences have been removed by subsequent erosion. On the other hand, there are some areas where sequences of this age are preserved (e.g. South Wales, Forest of Dean, English Midlands) and where unequivocal evidence of *M. macrophylla* has not been found. Similarly, well known upper Westphalian D sequences in Saar-Lorraine, Bohemia, Ukraine and northern Spain have all failed to yield this species.

DISCUSSION

Is Macroneuropteris a natural genus?

The frond architecture data provided in this paper, together with the cuticle evidence described by Cleal and Zodrow (1989), may be taken as providing the essence of *Macroneuropteris* Cleal *et al.*, 1990. *M. scheuchzeri* (Hoffmann) was also included by Cleal *et al.* in this form-genus, based partly on the cuticle evidence presented by Gothan (1915), Barthel (1961) and Cleal and Zodrow (1989). Some preliminary observations on the frond architecture of *M. scheuchzeri* have been made by Laveine (1967) and Laveine and Brousmiche (1982), but more complete material from Nord-Pas-de-Calais is now available and is currently being investigated. The initial results of this study appear to confirm that the architecture of the *M. scheuchzeri* frond has many features in common with that of *M. macrophylla*. For the other two species included by Cleal *et al.* (1990) in *Macroneuropteris* (*M. britannica* (Gutbier) and *M. subauriculata* (Sterzel)), no large frond segments have been documented in the literature and so their frond architecture is poorly understood; the revision of their generic position was proposed almost exclusively on cuticular evidence. In view of the importance that Cleal *et al.* (1990) and Cleal and Shute (1991) have placed on integrating gross morphology and cuticular evidence for establishing a robust taxonomy for these fronds, the systematic position of these two species must be regarded as questionable.

Are *M. scheuchzeri* and *M. macrophylla* closely related phylogenetically or is the morphological similarity merely an analogous solution to a common problem of adaptation? Neither species has yielded evidence of fructifications or rachis/stem anatomy. Nor is there any direct evidence of a gradation between the two species through time, as has for instance been demonstrated between *Neuropteris obliqua* (Brongniart) Zeiller and *Reticulopteris muensteri* (Eichwald) Gothan (Josten 1962; see also Zodrow and Cleal 1993; Cleal and Shute 1995). *M. macrophylla* must have evolved in habitats not represented in the fossil record, and that record can therefore provide no direct evidence of its ancestors. All that can be said is that both species share many features of morphology and epidermal structure, and that the balance of evidence tends to suggest that they represent a natural genus.

Macroneuropteris and Neuropteris compared and contrasted

Macroneuropteris is most similar to *Neuropteris*, as reconstructed by Zodrow and Cleal (1988) and Cleal and Shute (1991). The general architecture is identical, except that *Neuropteris* fronds are more divided (the primary pinna branches are at least tripinnate, instead of essentially bipinnate in *Macroneuropteris*). The pinnules of *M. macrophylla* are thus homologous with the segmented

tertiary pinnae of *Neuropteris* (Laveine 1967, p. 68; Laveine 1989, p. 44). The homology is confirmed in *M. scheuchzeri*, in which the pinnules often develop basal lobes, and thus could be interpreted as being transitional to tertiary pinnae. It is quite clear that the underlying frond architecture of the two frond-types is very similar and that they are almost certainly closely related. Following the arguments advanced by Laveine (1967), this might indicate that *Macroneuropteris* is merely a retarded growth form of typical neuropterid fronds. However, *Macroneuropteris* fronds were probably not significantly smaller than those of *Neuropteris heterophylla* (Laveine 1967; Cleal and Shute 1991). It also ignores the differences in epidermal structure, which Cleal *et al.* (1990) used as additional support for separating *Macroneuropteris* from *Neuropteris*.

Typical neuropterids often show a broad transitional zone in the upper and sometimes the lower regions of pinnae, where pinnules are changing to pinnae (e.g. Crookall 1959, pl. 26; Laveine 1967, pl. A, fig. 1c; Cleal and Shute 1991, figs 2–8). This is less pronounced in *Macroneuropteris*, and in *M. macrophylla* totally absent. In *M. scheuchzeri*, it is limited to the development of pinnae with one (anadromic) pinnule (usually designated as a lobe), then two (one anadromic and one catadromic) pinnules and, very exceptionally (on the primary rachis branches) three (two anadromic and one catadromic) pinnules. Some evidence of a transitional zone between pinnule and pinna is also offered by the '*Odontopteris lindleyana*' specimens illustrated in Laveine (1967, pl. 69, fig. 4, 4a) and Darrah (1969, pl. 26, fig. 3; pl. 34, figs 2–3; pl. 62, fig. 4). However, there is no direct evidence as to where such lobed pinnules occur in the frond, and so their morphological significance is not certain.

As *Macroneuropteris* has so many features in common with *Neuropteris* and the two are probably closely related, what is the justification for maintaining the generic distinction proposed by Cleal *et al.* (1990)? Laveine (1967, p. 314), while recognizing the distinctive morphology of the *Neuropteris* 'macrophylliens' species, argued that separating them in a new genus risked misleading non-specialists as to their natural relationship with *Neuropteris*. Whether or not this view is accepted probably depends to an extent on whether one is a 'lumper' or a 'splitter'. It must also be stated that Laveine's original view was based purely on gross morphology, as very little epidermal evidence had at that time been published, and the northern French fossils on which Laveine was then working do not yield cuticles. Cleal *et al.* (1990), when proposing the separation of the two genera, emphasized that it was based on an integration of cuticular and gross morphological evidence. It has also been found from a distributional analysis of neuropteroids in Europe (Cleal and Shute 1995), that species of *Neuropteris sensu* Cleal *et al.* (1990) and of *Macroneuropteris* appear to show different patterns of diversity, suggesting that they represent the foliar remains of separate groups of plants, probably sharing a common ancestry, but which reacted differently to environmental (e.g. edaphic) changes. Despite this, it is still clearly a subjective decision as to whether two groups of frond-types are separated generically; whether the separation continues to be maintained will depend on whether palaeobotanists find it useful for expressing their phylogenetic or distributional ideas.

Comparison of Macroneuropteris with other neuropteroid fronds

Laveineopteris is similar in most gross morphological characters to *Neuropteris*, except for the presence of large cyclopterid pinnules near the base of the frond. These cyclopterids are single pinnules attached directly to the primary rachis or primary rachis branches, and thus might appear comparable to the large ovoid pinnules attached to the primary rachis of *M. macrophylla*. However, these pinnules in *M. macrophylla* appear to be homologous to the pinnate foliage above the main dichotomy, being arranged in the same plane, and there being a gradational morphological series between them. In contrast, the cyclopterids of *Laveineopteris* have a quite different epidermal structure from the pinnate foliage (Cleal and Zodrow 1989). Furthermore, the larger laveineopterid cyclopterids in particular do not appear to have been originally orientated in the same plane as the rest of the frond, a feature that is shown by all of the larger specimens showing attached cyclopterids (von Roehl 1868, pl. 17; Carpentier 1930, pl. 8; Gothan 1953, text-fig. 8; Laveine 1967, pl. O,

fig. 1; pl. 45, fig. 3). Also, the strongly cordate base of many of these cyclopterids (e.g. Crookall 1959, pl. 27, fig. 7) is more compatible with them having originally been wrapped partially around the primary rachis. Unfortunately, there is no cuticular evidence for these large *M. macrophylla* pinnules, but their orientation and their gradation into normal-shaped pinnules suggests that they are not cyclopterids in the sense of Cleal and Zodrow (1989) and Cleal *et al.* (1990).

Certain specimens of *Macroneuropteris* (e.g. Text-fig. 2D; Crookall 1959, pl. 40, fig. 1) can appear very similar to *Paripteris* (e.g. Laveine 1967, pl. 71, fig. 2), such that the two genera might be thought to be synonymous. This is particularly suggested by the presence of intercalated pinnules on the penultimate rachises. It would be easy to believe that the pinnules are homologous structures in the two genera. However, the overall architecture of the fronds is fundamentally different (Laveine 1967, p. 68), most significantly in that the *Macroneuropteris* pinnae are imparipinnate (i.e. have just one apical pinnule), whereas *Paripteris* is paripinnate (i.e. pinnae have a pair of apical pinnules). Furthermore, *Paripteris* fronds never have lobate pinnules (Laveine 1967, pp. 247, 250; Laveine *et al.* 1993). It is true that neither does *M. macrophylla*, but the slightly more divided *M. scheuchzeri* frond shows the start of pinnule lobing by the development of one, two or, very rarely, three lobes (or incipient pinnules) at their base. This all reflects a major difference in the mode of frond construction for *Paripteris*, in which different orders of segmentation of the frond are produced exclusively by dichotomies and overtopping of the rachises, a construction that has been termed 'pseudo-pinnate' (Laveine *et al.* 1993), and suggests that *Paripteris* and its anastomosed veined counterpart *Linopteris* are only very distantly related to *Macroneuropteris*.

Using Macroneuropteris to understand the Neuropteris frond

The 'simplified' frond architecture of *M. macrophylla* can help in understanding the apparently more complex architecture of *Neuropteris* and *Laveineopteris* fronds. The reconstruction of the *M. macrophylla* frond shown in Text-figure 4 may be interpreted as follows. A primary rachis, bearing large pinnules, bifurcated to produce two equal primary rachis branches. Each of the primary rachis branches underwent a series of overtopped bifurcations, producing lateral ramifications (external and internal), organized and developed according to the available space within the frond. That the secondary pinnae are the product of overtopped dichotomies and were not merely produced by increasing the segmentation of the intercalated pinnules near the main dichotomy is clearly shown by specimen V.63416(a) (Pl. 1; Text-fig. 1B). If the frond was built only by a progressive increase in the differentiation of the laminar elements, then one should find, moving up from the dichotomy in this specimen, a gradation between the lowest, simple, entire pinnule and the first internal secondary pinna. This is obviously not the case and, in fact, the pinnules become slightly smaller near the first internal secondary pinna. The secondary pinnae must be the product of overtopped dichotomies and not a simple lateral mode of branching. The distal parts of the primary rachis branches in specimens V.63419(a) and V.63417 (Pl. 2, fig. 1; Pl. 3, fig. 2; Text-fig. 2A–B) also clearly show a more or less dichotomous, overtopped manner of branching.

By increasing the division of the secondary segments, it is possible to use this model to understand the construction of the *Neuropteris* fronds, as follows. A primary rachis, bearing ultimate pinnae (or possibly their homologous equivalents), bifurcated to produce two equal primary rachis branches. Each of the primary rachis branches underwent a series of overtopped bifurcations producing lateral ramifications (e.g. Laveine *et al.* 1977, text-fig. 6; Cleal and Shute 1991, fig. 2). These lateral ramifications appeared first on the external (catadromic) side of the primary rachis branches, where there was no special problem of available space. Inside the main dichotomy, the most proximal elements are ultimate pinnae, becoming progressively longer away from the main dichotomy as more space became available. However, these are not the products of overtopped branching, but merely the equivalent of the intercalated pinnae on the outwards facing side of the primary rachis branches (i.e. homologues of pinnules in the *M. macrophylla* frond). This is indicated by the absence of any intercalated foliar elements (which would presumably in this case be small lobate pinnules) between these most proximal, inwards facing pinnae on the *Neuropteris* frond. Only at a much more

distal position in the frond, when space became less of a problem in the centre of the frond, did overtopped branching occur to produce inwards-facing secondary pinnae, these being recognizable by the presence of short pinnae intercalated between them.

This general model appears to be further supported by the only known specimen of *Neuropteris guardinis* Grand'Eury (1890, pl. 22, fig. 2) as interpreted by Laveine (1967, text-fig. 14). The same mode prevails for the frond of *Odontopteris*, although because they were smaller, the overtopped dichotomies only produced secondary pinnae on the external side, the space available on the internal side having been too restricted.

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One of us (CJC) has recently been shown a specimen (SM X.27508) in the collections of the Sedgwick Museum, Cambridge, that clearly demonstrates overtopped branching in the distal part of a *M. macrophylla* primary rachis branch. This, therefore, confirms the reconstruction of this part of the frond given in Text-figure 3. This specimen will be documented in a later publication.

THE FIRST MESOZOIC SOLIFUGAE (ARACHNIDA), FROM THE CRETACEOUS OF BRAZIL, AND A REDESCRIPTION OF THE PALAEOZOIC SOLIFUGE

by PAUL A. SELDEN *and* WILLIAM A. SHEAR

ABSTRACT. The first Mesozoic solifuge, from the Early Cretaceous (Aptian) Crato Formation of Ceará province, Brazil, is described and named as *Cratosolpuga wunderlichi* Selden, gen. et sp. nov. and placed in the extant family Ceromidae. There are two previously described fossil solifuges: from Palaeogene Dominican amber and the Carboniferous (Westphalian D) Francis Creek Shale of Mazon Creek, Illinois. The latter specimen (*Protosolpuga carbonaria*), redescribed herein, is poorly preserved but provides evidence for the presence of the order in the Carboniferous.

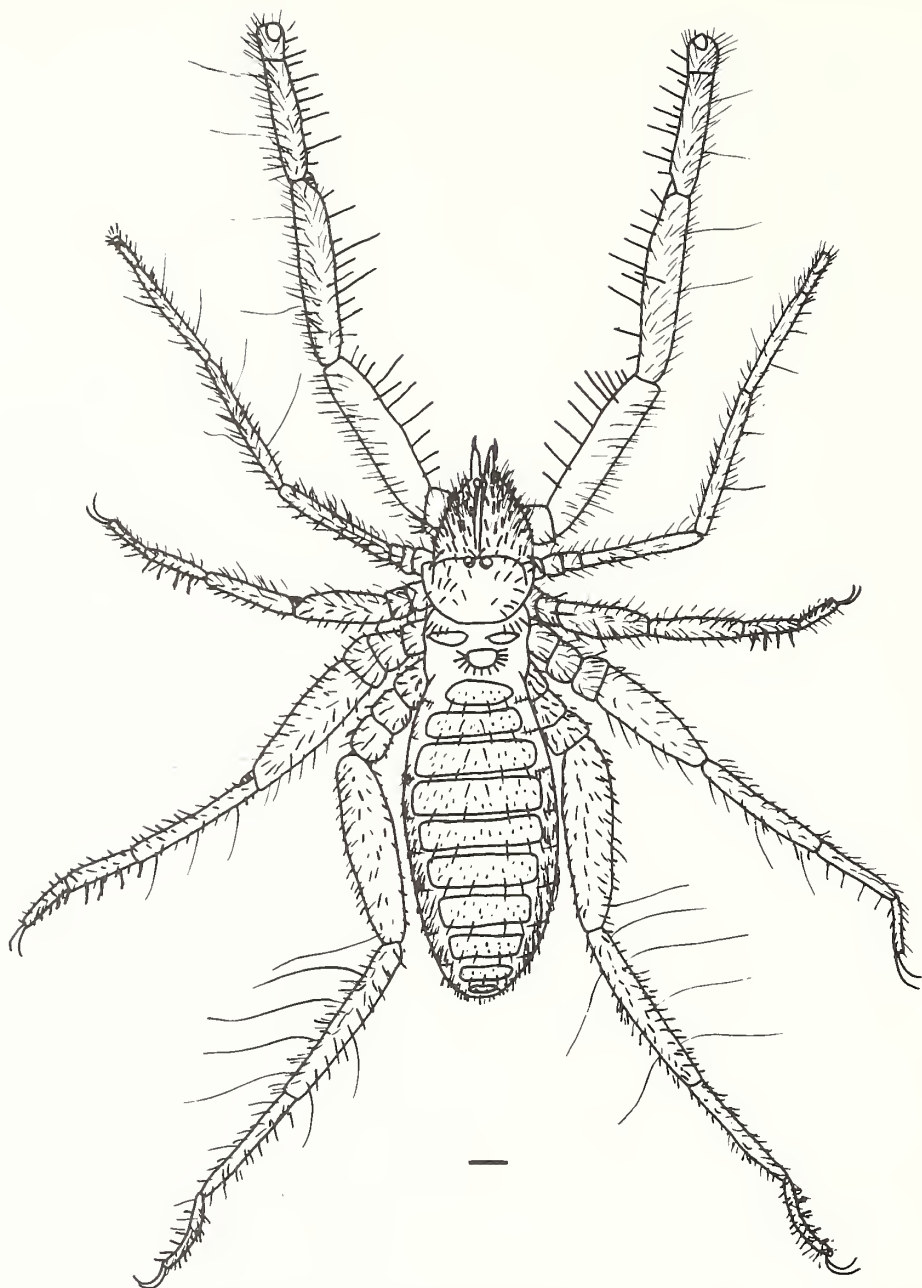
THE fearsome appearance of solifuges, with their enormous chelicerae and swift movements, ensures their familiarity among the inhabitants of desert regions of the world. None of their numerous vernacular names, for example camel-spiders, sun-spiders, Roman-spiders and wind-scorpions, is really appropriate. Most solifuges are nocturnal, but some emerge from their burrows to hunt in the daytime. Solifuges generally use their chelicerae for digging (Pocock 1897; Hewitt 1919, p. 19), although the short legs with rows of stiff spines of Hexisopodidae are adapted for rapid locomotion through sand (Cloudsley-Thompson 1977). The great speed of solifuges when disturbed is legendary, and with their profuse, long hairs, many species appear like tufts of thistledown blowing in the wind as they run across the ground. Solifuges are generalist predators: their prey includes spiders, grasshoppers, termites (Pocock 1897), and other insects (Punzo 1994), and even scorpions, mice, lizards, and birds (Cloudsley-Thompson 1977). Apparently, prey is detected and captured with the pedipalps, then killed and masticated with alternate, scissor-like movements of the powerful chelicerae, which lack venom.

Protosolpuga carbonaria Petrunkevitch, 1913, from the Upper Carboniferous (Westphalian D) of Mazon Creek, Illinois was the only fossil solifuge known until Poinar and Santiago-Blay (1989) described a specimen from Tertiary Dominican amber as *Happlodontus proterus*. *Protosolpuga* was described by Petrunkevitch (1913, p. 74) as being in a very poor state of preservation. Our study confirms this, and gives a new interpretation of the fossil, which is nevertheless just recognizable as a solifuge.

A new solifuge is described here (Text-fig. 1), from two specimens preserved in exceptional detail in the Crato Formation, Cretaceous of Brazil. They are the first known from Mesozoic strata. The only previous records of Brazilian solifuges are Recent Ammotrechidae and Mummuciidae from the south-east of the country (Maury 1984). Indeed, north-eastern Brazil is farther geographically from any previous solifuge record within the tropics.

Terminology

The ordinal name Solifugae is used in preference to Solpugida on the recommendation of the Centre International de Documentation Arachnologique. For solifuge terminology, we have mainly followed Muma (1951). A recent reinterpretation of solifuge appendages by Shultz (1989, 1990) concluded that the classical terminology applied to solifuge podomeres was based on erroneous



TEXT-FIG. 1. Reconstruction of *Cratosolpuga wunderlichi* Selden, gen. et sp. nov., Cretaceous (Aptian), Crato Formation, Ceará Province, Brazil, illustrating general appearance of solifuges. Scale bar represents 1 mm.

homology. We follow Shultz's terminology here, and a comparison of the terms is given in Table 1. Description of the Carboniferous solifuge was prepared by WAS; that of the Cretaceous solifuge by PAS, who is also responsible for the Systematic Palaeontology. Abbreviations used in the Text-figures are as follows:

I–10	opisthosomal sternite numbers	mp	mesopeltidium
I, II, III, IV	leg numbers	mtp	metapeltidium
ar p	arcus posterior (of parapeltidium)	op	opisthosoma
ch	chelicera	operc	operculum
cx	coxa	pa	patella
el	exterior lobe (of propeltidium)	pd	pedipalp
f fi ch	fixed finger of chelicera	pp	propeltidium
fe	femur (legs I, II)	st	sternal plate between coxae I (tritosternum)
fe1, fe 2	basifemur, telofemur (legs III, IV)	ta	tarsus of pedipalp
fl	flagellum	ta1, ta2	basitarsus, telotarsus of legs
m fi ch	movable finger of chelicera	ti	tibia
ma	malleolus (racquet organ)	ti trich	tibial trichobothrium
med pl	median plagula (of parapeltidium)	tr	trochanter

TABLE 1. Comparison of Shultz's (1989) solifuge podomere terminology with that of Roewer (1934)

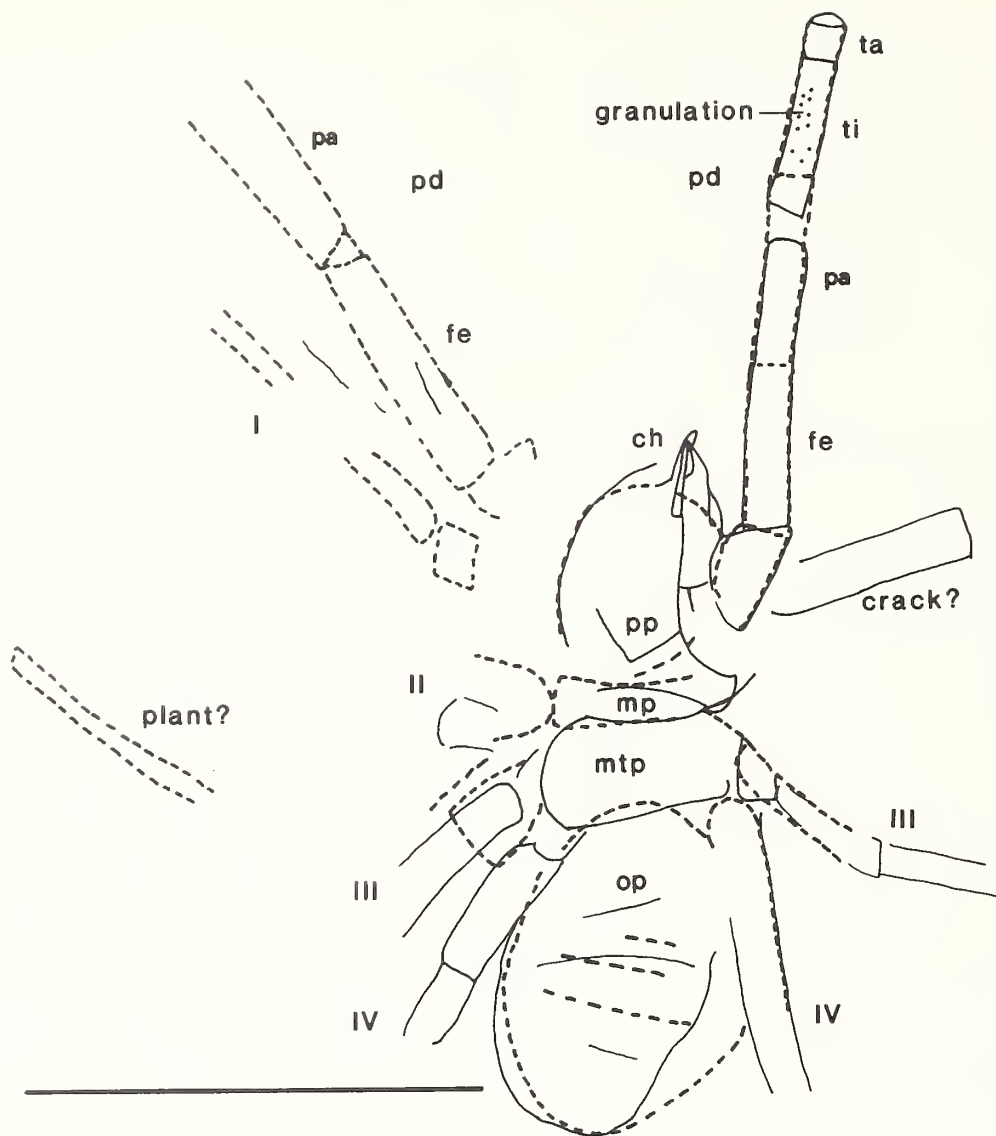
Pedipalp		Legs I and II		Legs III and IV	
Shultz	Roewer	Shultz	Roewer	Shultz	Roewer
Coxa	Coxa	Coxa	Coxa	Coxa	Coxa
Trochanter	Trochanter	Trochanter	Trochanter	Trochanter	Trochanter I
Femur	Femur	Femur	Femur I	Basifemur	Trochanter II
Patella	Tibia	Patella	Femur II	Telofemur	Femur I
Tibia	Metatarsus	Tibia	Tibia	Patella	Femur II
Tarsus	Tarsus	Basitarsus	Metatarsus	Tibia	Tibia
Apotele	Pretarsus	Telotarsus	Tarsus	Basitarsus	Metatarsus
—	—	Apotele	Pretarsus	Telotarsus	Tarsus
—	—	—	—	Apotele	Pretarsus

*PROTOSOLPUGA CARBONARIA**Material*

The holotype and only known specimen of this arachnid (Peabody Museum, Yale University, 00155/B1336; Pl. 1, figs 1–2; Text-fig. 2) comes from the Carboniferous (Westphalian D) of Mazon Creek, Illinois. It is preserved in a siderite (iron carbonate) nodule characteristic of that locality, with both halves preserved. Despite the poor preservation, each half of the nodule preserves a mixture of dorsal and ventral features. Petrunkevitch's drawing (1913, fig. 40) is highly diagrammatic and shows a few features that cannot now be seen on the specimen. Conversely, some features that appear obvious on the specimen now are not on his drawing. On one half, the most obvious feature is a large structure with deformed small ridges at the distal end, which Petrunkevitch interpreted as the chelicerae; because most of the structures that can be made out on this half appear to be ventral ones, this side is here designated the ventral half, and the other the dorsal half. Petrunkevitch's drawing is a composite of both surfaces, with some features shown on the dorsal half reversed.

Morphological interpretation

The ventral half preserves the body and at least six appendages of an arachnid. Anteriorly, the fossil displays a small arrangement of twisted ridges forming a distal structure on a pear-shaped mass that appears to have a central dividing groove. This was interpreted by Petrunkevitch (1913) as the large chelate chelicerae of a solifuge; the ridges to which he referred were thought to represent the



TEXT-FIG. 2. Composite camera lucida drawing of *Protosolpuga carbonaria* Petrunkevitch, 1913. Holotype, Peabody Museum 00155/B1336; Upper Carboniferous (Westphalian D), Francis Creek Shale; Mazon Creek, Illinois. Solid lines, ventral side; dashed lines, dorsal side. Scale bar represents 10 mm.

cheliceral fingers. Petrunkevitch referred to and illustrated 'a row of punctuations' on each finger, but these cannot now be detected. Behind the supposed chelicerae, the outlines of a broad plate can be discerned, separated from the cheliceral bases by a short space. This may be a dorsal structure, the tergite of the metapeltidium. The abdomen is an oval roughly twice as long as wide, with only a few vague lines possibly indicating segmentation. In this area there is some carbonized material and several clusters of pyrite crystals. Lateral to the chelicerae on one side is a large pedipalp coxa, from which extend distal segments of the leg-like pedipalp. Little detail is visible and the segmentation of the pedipalp cannot be made out clearly on either half of the nodule. However, at

the end of the preserved portion, as Petrunkevitch noted, there is a short podomere about as wide as long, with a distal concavity. This is consistent with the small pedipalp tarsus of a solifuge, which bears a distal, eversible membranous sac. If this interpretation is correct, the next proximal segment is the tibia. On the ventral half, a series of small granulations (Text-fig. 2) can be seen, and these are reflected on the dorsal half by a series of small pits in the corresponding positions. Stout spines are borne on the tibiae of some living solifuges, and these pits may represent their sockets. The other appendages that are preserved are presumed to be legs; the presence of four pairs can be confirmed by combining information from both halves.

On the dorsal half, the chelicerae do not appear as clearly as on the ventral half; one sees only a rounded mass with a vague outline. However, under alcohol, contrast between small areas of carbonized material and the reddish matrix is enhanced, and there appears to be a transverse divide which could separate the chelicerar bases from the propeltidium. Approximately in the anterior midline is a small carbonized knob; this is in the position of the median eye tubercle in living solifuges. Petrunkevitch (1913) stated flatly 'eyes absent' but presumably he meant that he could detect no evidence for eyes. Behind the possible propeltidium is a narrow band which could be the tergite of the mesopeltidium. The metapeltidium does not appear on this half of the nodule. The abdomen looks about the same as on the ventral half. The dorsal half preserves more of the legs and parts of both pedipalps. At least the first leg is more slender than the pedipalps, but the third leg also appears as gracile as the first. What appear to be the remnants of fourth legs are about half as robust. On both halves there is an elongate structure some distance from the specimen which was obviously considered by Petrunkevitch to be a distal leg segment. However, it has quite a different texture from the rest of the fossil and is probably a plant fragment.

The chelicerar punctuations depicted by Petrunkevitch cannot be seen. Mysteriously, he mentioned 'three free thoracic segments', but in living solifuges there are only two, the meso- and metapeltidia. Petrunkevitch's drawing actually shows four, not three, of these segments, but there is no evidence for any more than the expected two, taking into account that both halves of the nodule preserve both dorsal and ventral structures. The 'even segmentation' of the pedipalps is not really clear; at least one of the 'joints' is due to a crack in the matrix. On the right side of Text-figure 2 the large cylindrical structure extending from the pedipalp coxa at about 70° to the pedipalp, and considered by Petrunkevitch as part of a leg, is very probably due to cracking of the nodule. Three short, narrow pieces, considered by Petrunkevitch as legs, are found in his illustration. One of these is the aforementioned bit of plant debris; the other two cannot be found under any conditions of lighting. These were probably the evidence for Petrunkevitch's characterization of the second legs as 'considerably thinner than the others'. In fact, it would appear that only the coxa of the second leg on the right side is preserved, so nothing can be said about their relative robustness. Petrunkevitch also depicted the first leg (on the left side of Text-fig. 2) as nearly as robust as the pedipalp; in reality it is only about half as thick. The segmental lines shown by Petrunkevitch and his description of the abdomen as consisting of seven segments is not supported by evidence. There are few possible segmental lines visible and even these could be attributable to folding of the soft abdomen or other factors. In any case, modern solifuges have a typical 11-segmented abdomen, and it would be remarkable if this were not the case in the Carboniferous forms as well.

Discussion

Of the orders of Arachnida supposedly known from the Carboniferous, only spiders, trigonotarbid and solifuges (represented only by the present specimen) have leg-like pedipalps. Spider and trigonotarbid pedipalps are shorter than the legs. *Protosolpuga carbonaria* clearly shows a leg-like pedipalp that is equal to or even larger than the walking legs. In addition, a small, button-like tarsus appears to be present. If the interpretation of the anterior structure as the chelicerae is correct, and if there are two free thoracic segments, this is additional evidence that the specimen really does represent a solifuge.

The level of preservation is so poor that the fossil tells us little about solifuge evolution. Perhaps it should be expected that, like other orders of arachnids, Solifugae had assumed a fully modern form by Carboniferous times.

THE CRETACEOUS SOLIFUGE

Geological setting

The solifuge specimens originate from the Crato Formation (*sensu* Martill 1993), a sequence of laminated, organic-rich micrites (Plattenkalk), which crop out on the north side of the Chapada do Araripe in north-eastern Brazil, dated tentatively as Aptian (Maisey 1990; Martill 1993). The Crato Formation is rich in insects (Grimaldi 1990), and also contains the small fish *Dastilbe*, land plants (including angiosperms), other arachnids (including spiders, scorpions, uropygids and opilionids), frogs, and bird feathers, but no terrestrial or flying reptiles (Martill 1993). The palaeoenvironment is presumed to be lacustrine, the majority of the biota is allochthonous, being blown or washed into the lake or, if aquatic, subject to mass mortality (Maisey 1990; Martill 1993).

The Crato Lake formed within the Aquatic Basin, one of a number of fault-bounded Mesozoic basins in what is now north-eastern Brazil which occupied the Atlantic rifting zone between Africa and South America in early Cretaceous times. The fault lines in this part of Brazil align with the Benue Trough and other lineaments in West Africa, and it is suspected that these older faults were reactivated to become transforms at the onset of rifting (Berthou 1990). As far as the solifuge is concerned, its contemporaries could have moved freely overland between what are now the African and American continents.

Taphonomy

No chemical analyses were carried out on the specimens, but, in comparison with the insects preserved in the Crato Formation (Grimaldi and Maisey 1990), we presume that the solifuge fossils are preserved in goethite (hydrated iron oxide) in a matrix of nearly pure calcite mud with clots of pyrolusite. The goethite is a tan colour which is darker where thicker and thus reflects the depth of coloration seen in the original cuticle. The mineralization appears to have replaced the original organic material in great detail, so that spines, bristles, and fine trichobothria can be traced accurately in the matrix. Where absent, the former presence of spines and trichobothria is indicated by spine bases and bothria on the cuticle surface. The membrane on the cheliceral flagellum of the holotype is preserved almost intact. Where the podomere cuticle is broken through on the femur of the right pedipalp of the holotype, a structure interpreted as a tendon can be seen. It is clear that the preserved parts represent material of originally cuticular composition (e.g. tendons) because most of the fossil is crushed to some extent, and no evidence of internal soft tissues (e.g. muscles) can be seen.

EXPLANATION OF PLATE 1

- Figs 1–2. *Protosolpuga carbonaria* Petrunkevitch, 1913. Holotype; Upper Carboniferous (Westphalian D), Francis Creek Shale; Mazon Creek, Illinois; Peabody Museum 00155/B1336. 1, part (mainly ventral). 2, counterpart (mainly dorsal); $\times 4.5$. See Text-figure 2 for explanation.
- Fig. 3. *Cratosolpuga wunderlichi* Selden, gen. et sp. nov. Additional (juvenile) specimen; Cretaceous (Aptian), Crato Formation; Ceará Province, Brazil; SMNK 1268 PAL in Staatliches Museum für Naturkunde, Karlsruhe; dorsal view of ventral structures; $\times 9.5$. See Text-figure 3 for explanation.
- Fig. 4. *Cratosolpuga wunderlichi* Selden, gen. et sp. nov. Holotype; Cretaceous (Aptian), Crato Formation; Ceará Province, Brazil; Sol 1 in the Wunderlich Collection; dorsal view of prosoma omitting distal parts of appendages; $\times 11.4$. See Text-figure 4 for explanation.



Material and methods

The holotype (Pl. 1, fig. 4; Pl. 2; Text-figs 4–6) consists of a single slab of laminated, pinkish buff limestone with the fossil on the presumed upper surface. The lower half of the slab is brownish buff limestone, and the lower surface is thickly strewn with clots of dendritic pyrolusite. No other fossils are present on the slab. The pinkish upper half of the slab has been broken, and repaired with glue. The break is visible as a sinuous crack across the middle of the specimen, cutting the proximal podomeres of legs III and IV and the basitarsus and telotarsus of right leg II. Some careful preparation was necessary to expose fully details of the specimen, such as the lateral parts of the chelicerae and propeltidium and tarsal claws. This was accomplished using a combination of dilute hydrochloric acid (used sparingly and of only little aid to preparation) and mechanical scraping. A very fine, steel hypodermic needle was connected to the polythene tubing of an air pump of the type intended to aerate small indoor aquaria. The matrix was loosened gently using the bevelled tip of the hypodermic needle under the binocular microscope ($\times 40$ – $\times 60$). The advantage of this over a simple fine needle is that loosened particles of matrix are blown away immediately, revealing the specimen beneath. Also, the loose grains themselves gently dislodge other particles around the area, so that the working site is always clean.

The second specimen (Pl. 1, fig. 3; Text-fig. 3) is about one-quarter the size of the holotype, and is presumed to be a juvenile. It is preserved as an external mould with fragments of cuticle, spines and setae adhering. It preserves the ventral side of the prosoma and abdomen and all appendages. It therefore complements the holotype in providing details of parts of the body which are missing from the latter. Little preparation was carried out on the second specimen.

Modern solifuges were studied for comparative purposes. Undetermined specimens of families Solpugidae and Galeodidae were available, together with adult males of Solpugidae, *Ceroma ornatum* Karsch, 1885 (Ceromidae) and *Blossia sabulosa* (Lawrence, 1927) (Daesiidae). A female ceromid, lacking data but identified using Roewer (1934) as *C. ornatum*, was also studied.

Morphological interpretation

The fossils appear remarkably modern in aspect; the morphology is essentially similar to that of a modern solifuge, and they have been interpreted in this light (Text-fig. 1). A few critical features are discussed below, with reference to the holotype unless stated otherwise.

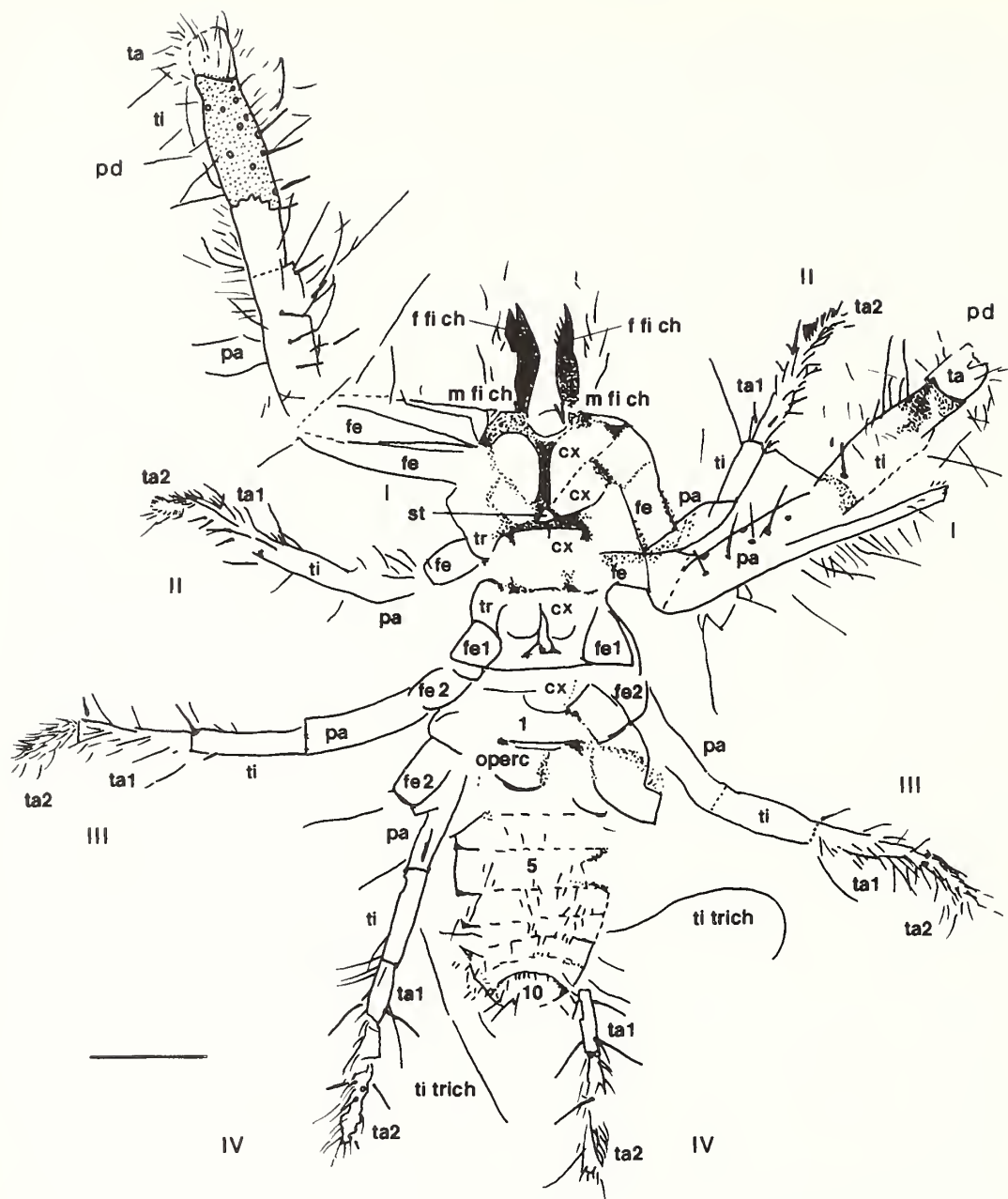
Propeltidium and associated tergites. The propeltidium of *Cratosolpuga* gen. nov. is wider than long. The anterior margin is very slightly recurved. The anterior edge is clearly rebordered, a feature which continues posterolaterally adjacent to the exterior lobe. The exterior lobe is strongly raised into a pyramidal shape. The exterior lobe is clearly separated from the main part of the propeltidium except posteriorly; presumably in life it was free except posteriorly, an arrangement found in numerous families of modern solifuges. The posterior margin is procurved into a semicircle. The boundaries of the tergites posterior to the propeltidium are not entirely clear. The most obvious structure is a pair of high, steep-sided transverse ridges. These ridges almost certainly correspond to the anterior edges of the left and right arcus posterior of the propeltidium. Anterior to the ridges is a crescentic area which corresponds to the median plagula and arcus anterior of the propeltidium. Behind the propeltidium the ridges fall steeply to the basal podomeres of leg III and, medially, a semicircular structure with radiating spines which corresponds to the mesopeltidium (= penultimate prosomal tergite).

EXPLANATION OF PLATE 2

Fig. 1. *Cratosolpuga wunderlichi* Selden, gen. et sp. nov. Holotype; Cretaceous (Aptian), Crato Formation; Ceará Province, Brazil; Sol 1 in the Wunderlich Collection; complete specimen seen from dorsal aspect; $\times 4.7$. See Text-figure 5 for explanation.

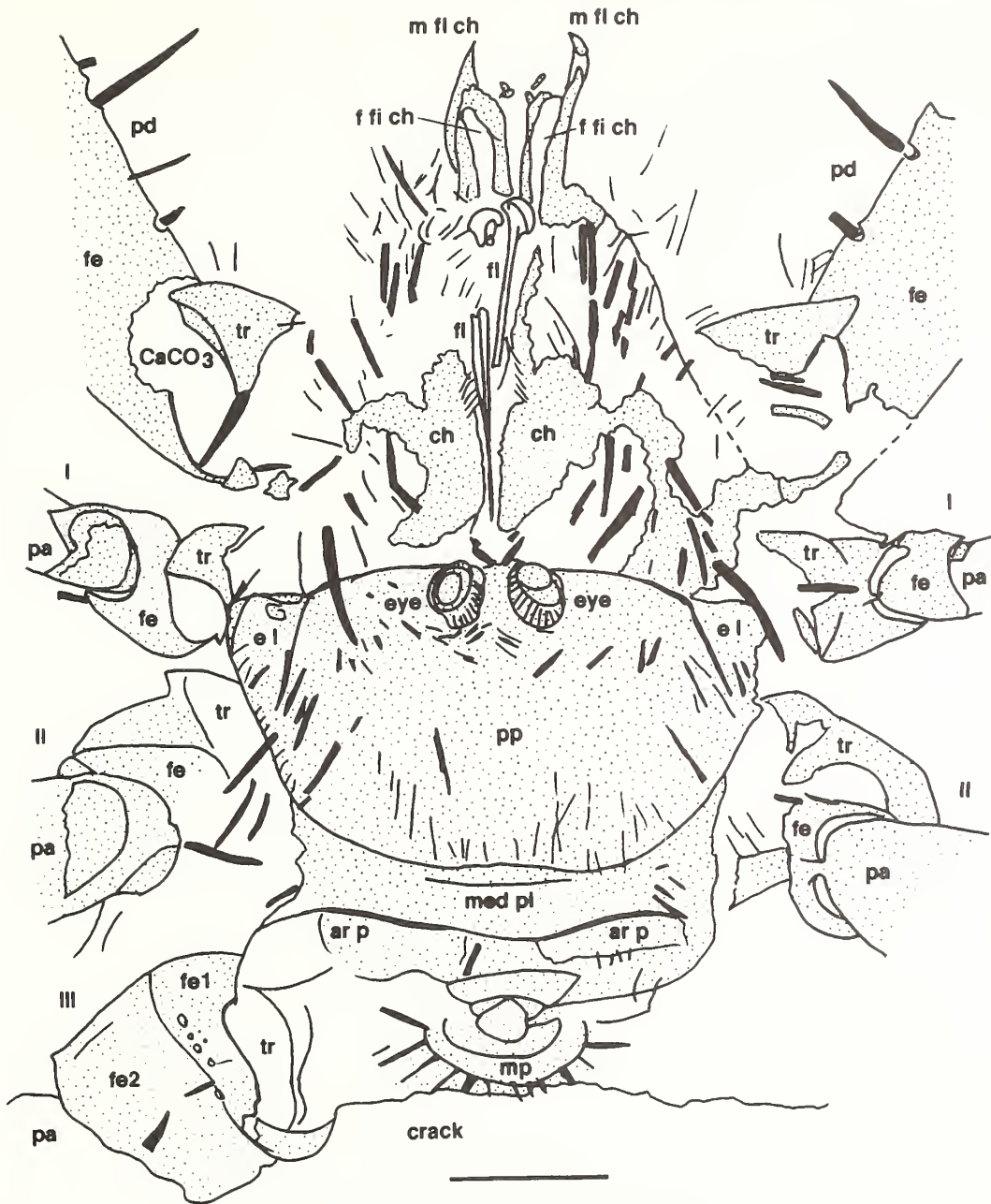


SELDEN and SHEAR, *Cratosolpuga*



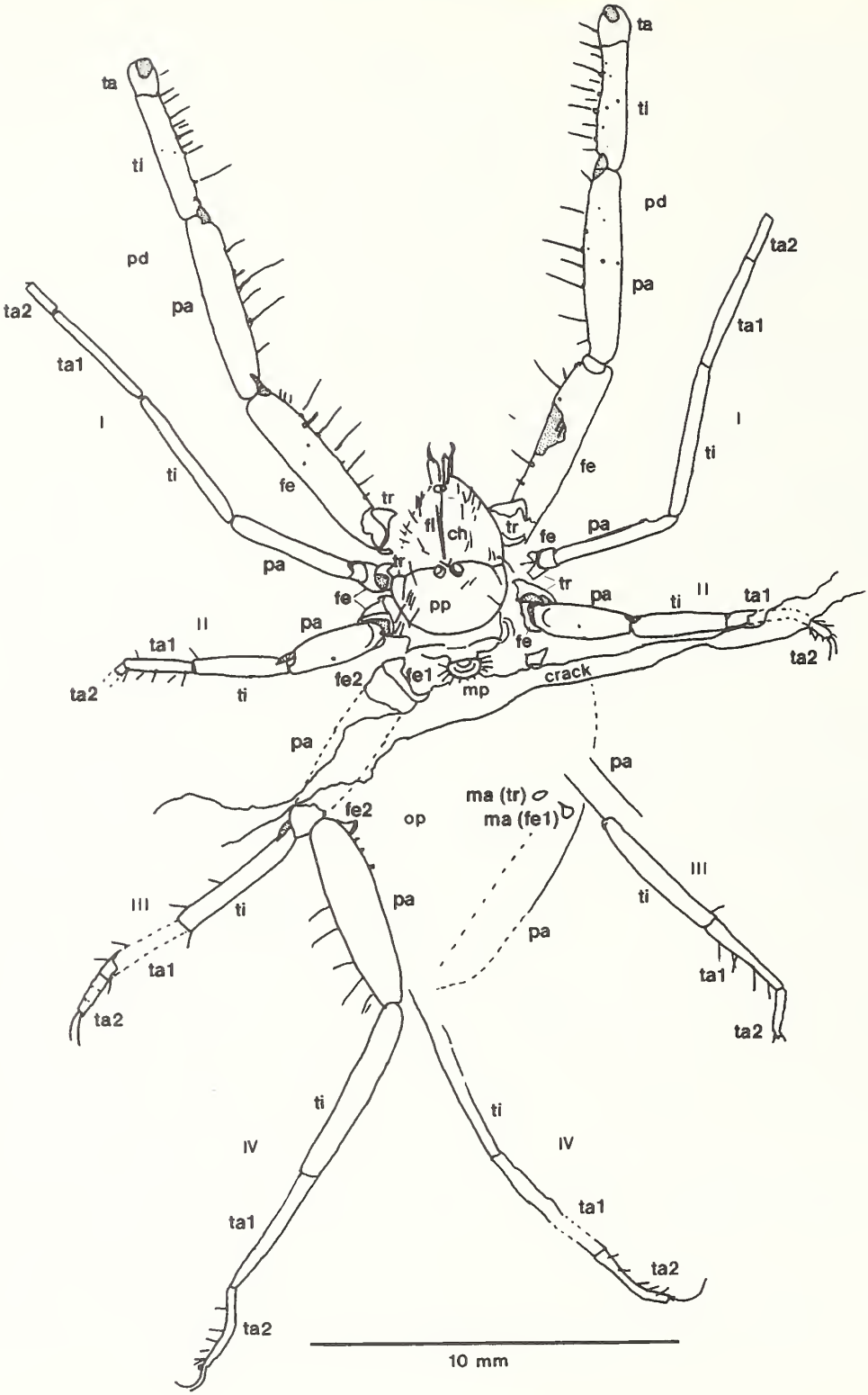
TEXT-FIG. 3. Camera lucida drawing of *Cratosolpuga wunderlichi* Selden, gen. et sp. nov. Additional (juvenile) specimen; Cretaceous (Aptian), Crato Formation, Ceará Province, Brazil; SMNK 1268 PAL in Staatliches Museum für Naturkunde, Karlsruhe. See Plate 1, figure 3. Scale bar represents 1 mm.

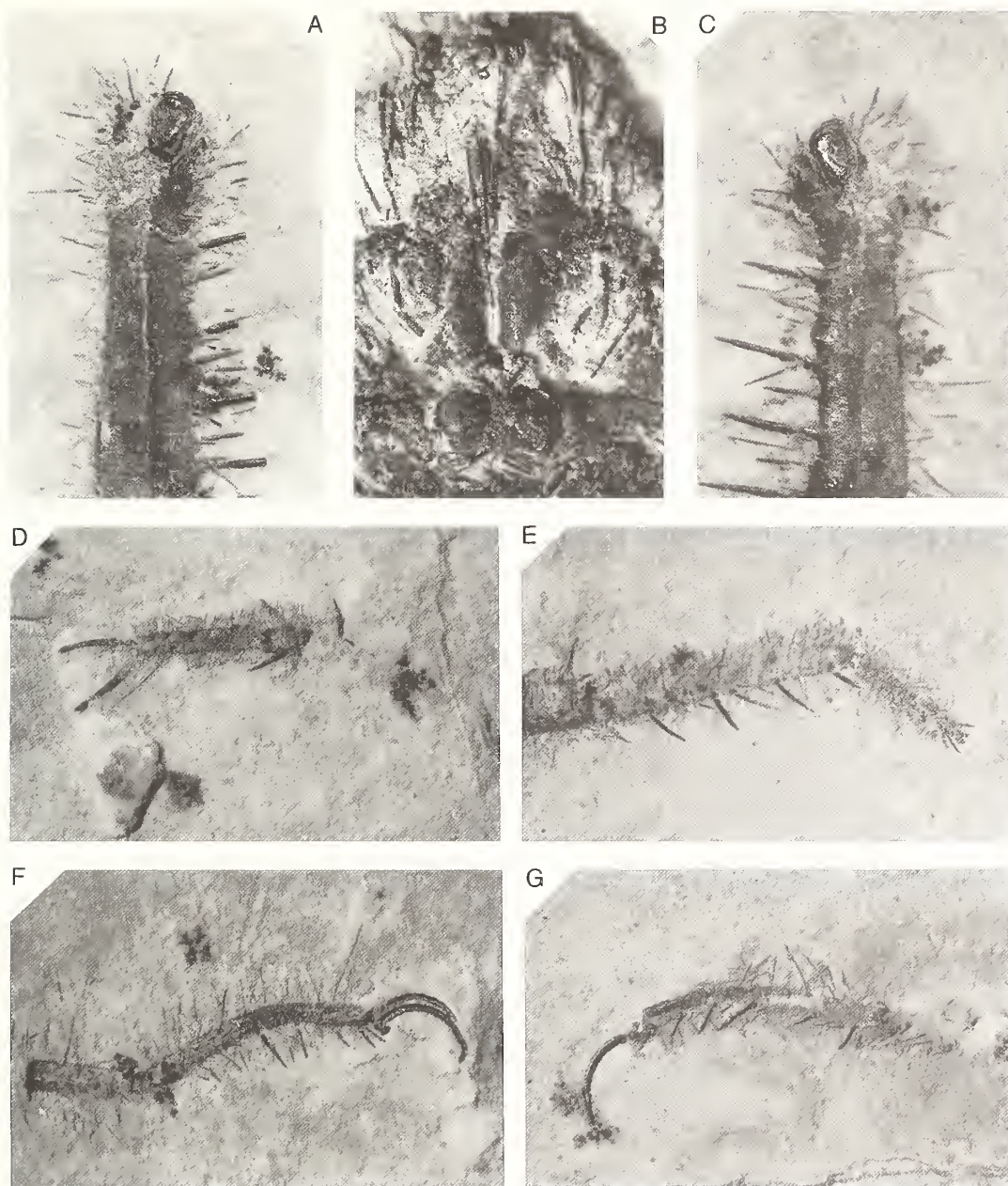
Chelicerae. The chelicerae were clearly bulbous in the proximal part, but narrow considerably at the base of the dorsal fixed finger. The dorsal side of the fixed finger has a concavity which contains calcite grains; the distal (anterior) end of the fixed finger appears to be broken off. This observation leads to a number of possible conclusions.



TEXT-FIG. 4. Camera lucida drawing of prosoma (omitting distal parts of appendages) of *Cratosolpuga wunderlichi* Selden, gen. et sp. nov. Holotype; Cretaceous (Aptian), Crato Formation; Ceará Province, Brazil; Sol 1. Dotted regions are exposed cuticle (preserved in goethite); strong spines shown in black; flagella ornamentation not shown, for clarity. Scale bar represents 1 mm.

First, there may have been a real concavity in life; this would explain the grains of matrix within the concavity. Some eremobatids (Muma 1951) bear dorsal concavities on the fixed finger; such concavities are normally not on the dorsal side of the finger, however. Secondly, it could represent





TEXT-FIG. 6. *Cratosolpuga wunderlichii* Selden, gen. et sp. nov. Holotype; Cretaceous (Aptian), Crato Formation; Ceará Province, Brazil; Sol 1. A, C, distal tibia and tarsus of pedipalp. A, left $\times 20$; C, right $\times 23$. B, anterior carapace margin with eyes, and basal chelicerae showing male flagella; basal section of whip of left flagellum is missing; whips disappear into matrix between cheliceral bases; $\times 23$. D-G, tarsi of legs left III, right III, left IV and right IV, respectively; showing basitarsal spines (leg III), hairs and trichobothria, and telotarsal claws (missing from right III) with distal joint; $\times 15$.

TEXT-FIG. 5. Camera lucida drawing of *Cratosolpuga wunderlichii* Selden, gen. et sp. nov. Holotype; Cretaceous (Aptian), Crato Formation, Ceará Province, Brazil; Sol 1 in the Wunderlich Collection. See Plate 2. Scale bar represents 10 mm.

a dorsal flagellum as seen in Gylippidae (e.g. Roewer 1934, figs 228–229, 233–234); the feature in the fossil appears more substantial than such membranous flagella, however. Thirdly, the fixed finger may have been broken or crushed and matrix (or calcite-bearing fluids, perhaps) has entered the finger. Fourthly, the dorsal side of the fixed finger is crushed down into the finger so that its dorsal side appears concave, with matrix filling the concavity. Of the second and third possibilities, the latter appears to be the more likely, since observation of modern solifuges shows that on the dorsal side of the fixed finger the cuticle is rather thinner than the lateral parts, and similar crushing of the dorsal side of the cheliceral hand can also be seen.

Dorsal and lateral parts of the movable finger can be seen in the holotype, especially on the left side, and these lie slightly outside the fixed finger and distally curve mesially towards the tip of the fixed finger. The movable finger is preserved on the second specimen, together with fragments of the fixed finger.

Flagellum. The chelicera of the holotype bears a structure known only in adult male solifuges: the flagellum. This is actually a complex of structures, which varies greatly between and within solifuge families (Roewer 1934). In some, the dorsal side of the base of the fixed finger bears a curious horn or projections. In others, there is a bunch of large setae, which may be plumose or distally expanded, and such setae may extend onto the movable finger. In many genera there is a single organ (flagellum proper, presumably a highly modified seta) which is commonly associated with groups of modified setae. This latter type is found in the fossil genus. In modern solifuges the flagellum proper may be a curved or coiled whip-like structure or may be shorter and membranous. There may be a whip-like structure with a membrane, and occasionally a variety of such structures occur on the same animal. The flagellum may be fixed or movable, in which case the movement is generally paraxial. The function of the flagellum has not been clearly established. Though confined to the male sex, it has not been observed taking part in copulatory activities.

The flagellum of *Cratosolpuga* is a straight, styliform structure on a bulbous base, with a narrow strip of membrane running the length of the spine (Text-fig. 6b). The membrane appears to have been widest at the base, where remnants of its broken edge on the base suggest it partly enveloped the base. Distal to the base, the stiff membrane is curved in a gutter-like arrangement. Gradually, towards the tip of the flagellum, the membrane dominates over the flagellar shaft, and eventually the membrane edge forms the acicular tip to the flagellum. The bulbous base is clearly set off from the chelicera, which could be evidence for its movability, but members of the family Solpugidae bear a flagellum with a bulbous base, clearly set off from the chelicera which is immovable.

The male flagellum is very distinctive and differs between species. It is a good specific character, and is always figured when new species are described in which males are known (indeed, it is not always possible to identify female solifuges). The flagellum of *Cratosolpuga* resembles somewhat that of some southern African *Blossiola* species (e.g. *B. hessei* Lawrence, 1929), in which the membrane is narrow and runs along the length of the styliform flagellum which is bent slightly only near the tip. The flagellum of these daesiids is movable. The bulbous base of the flagellum resembles that of the Solpugidae, but in this family the flagellum is fixed, and the distal, whip-like part of the flagellum always runs anteriorly for a short distance before curving backwards (the whip passes directly backwards in *Cratosolpuga*). There is no membrane running along the solifuge flagellum, which is tubular. In Ceromidae, the flagellum is movable on a bulbous base, the shaft is long, runs nearly directly backwards, and bears a thin strip of membrane running along the flagellum length. The flagellum of the ceromid *Ceroma ornatum*, studied by PAS, is very similar to that of *Cratosolpuga*, except that it curves somewhat and reaches back beyond the base of the chelicera.

Coxosternal region. The coxosternal region is seen only in the juvenile specimen (Text-fig. 3). The pedipalp coxae are large, directed anterolaterally, and come close together along straight mesial margins. The coxae of leg I are also directed anterolaterally; they do not meet mesially, but are separated by a small triangular area, presumably occupied by a sclerite in life. Sørensen (1914, pl. 1, fig. 4, *ste*¹) and Roewer (1934, fig. 80, *St*₁) figured a sternite (tritosternum according to Roewer)

in this position, and a similar structure can be seen in *Ceroma ornatum*. According to Sørensen, this conceals the suboesophageal ganglion. The more posterior coxae appear to be laterally directed, with clear gutters separating the coxae of legs II and III.

Pedipalp. The pedipalp in Solifugae consists of coxa, trochanter, femur, patella, tibia and tarsus. The limb joints seen in the fossil are almost identical to the examples shown by Roewer (1934). For example, at the pedipalp patella–tibia joint of *Cratosolpuga*, there are some approximately triangular areas of shiny, wrinkled cuticle to the mesial side of the articulation point which represent the areas labelled Gleitflächen on Roewer's (1934) figure 56, which shows the same joint in *Solpuga venator*. Examination of a specimen of *Galeodes* revealed that this cuticle is somewhat leathery, stiff but neither membranous nor rigid, and the triangular areas fold against one another rather like the zigzag folding sides of a piano accordion or an expanding document case. The true arthrodial membrane in the fossil is hidden beneath these areas of leathery cuticle.

The pedipalp tarsus of *Cratosolpuga* is short, somewhat bulbous, and broader than the tibia (Text-fig. 6A, c). The tibia–tarsus joint is distinct, especially on the mesial side of the dorsal surface. Possibly the tarsus was movable to some extent. At the inner distal tip of the tarsus is a raised area of dark, shiny, wrinkled cuticle which represents the sucker organ.

Legs. The legs of *Cratosolpuga* are rather long; the leg formula is 4132. The first leg is, as in most solifuges, long and thin, and used as a tactile organ similar to the pedipalps in other arachnids. It consists of coxa, trochanter, two femora, tibia, basitarsus and telotarsus. This leg bears no spines, only short and long fine hairs and bristles. The number of leg I tarsal claws is used in the family diagnoses of solifuges (Muma 1976); they vary from 0–2, and there is some variability within families. Early workers were unaware that these claws could be used for phylogenetic purposes, particularly as they may be tiny and hidden amongst setae and spines; for this reason they were occasionally overlooked. In *Cratosolpuga*, there is evidence for at least one small claw, in the form of a tiny, transverse spine at the distal tip of the telotarsus on the left side; on the right side, about three transverse bristles can be seen. So it is possible that these are merely bristles at the tip of the telotarsus preserved transversely, rather than true claws.

Leg II consists of coxa, trochanter, two femora, tibia, basitarsus and telotarsus. The proximal podomeres are directed upwards, so that they present their distal joints on the fossil. This is the shortest leg. The tibia bears a distal, slightly curved, spine. The basitarsus bears three slightly distally curved spines on its presumed dorsal surface, and between these are two more similar spines slightly removed from the main row towards the posterior surface. This spination is found on a number of modern solifuges. The telotarsus is poorly preserved on the left side of the holotype, but the right side shows a pair of long, curved naked claws with a joint near the tip. The telotarsus bears pairs of spines ventrally. More than one pair of spines may be present on each tarsomere, so it is impossible to count the number of tarsomeres by counting spine pairs. However, since each tarsomere generally bears at least one pair of spines, each spine pair could represent one tarsomere. Thus a maximum of four tarsomeres may be present in the telotarsus of leg II, but the lack of evidence for any joints (which are conspicuous elsewhere on the limbs) suggests that only a single tarsal segment was present.

Legs III and IV consist of coxa, trochanter, basifemur, telofemur, patella, tibia, basitarsus and telotarsus. Both legs are quite long. The telotarsus of leg III is not well preserved on the holotype, but the lack of joints suggests that only a single segment is present; if tarsomeres are present then there is a maximum of four. The telotarsus of leg IV is better preserved, and the lack of joints indicates a single segment. A pair of long, curved, naked claws with a joint near the tip is present on the tarsi of legs III and IV, as on leg II. Tarsal claws cannot be seen on the juvenile specimen; the visible tarsi are thickly clothed with setae (Text-figs 3, 6D–G).

The proximal podomeres of leg IV are poorly preserved on the holotype, but remnants of two racquet organs (malleoli) are preserved on the right side. In living solifuges, malleoli occur on the coxa (two), trochanter (two) and basifemur (one). Judging from their position, the malleoli on the

fossil represent the distal one of the trochanter and the single one of the basifemur. Only a small part of the telofemur is preserved on the left side. This podomere must be very short on the dorsal side of the holotype, given the length of the dorsal side of femur 2 (seen on the left side) and the position of the posteriormost malleolus which would have been situated on the basifemur. On the juvenile specimen, long trichobothria can be seen extending from tibiae IV (Text-fig. 3).

Opisthosoma. The abdomen is well preserved only on the juvenile specimen (Text-fig. 3). Ten segments can be counted from between the coxae of the fourth leg to the rear of the animal. The second of these appears to consist of a pair of lobes, and probably represents the operculum. The following segments are revealed by paired dark lateral corners and rows of setae. The more anterior post-opercular segments appear to be rectangular, the more posterior become increasingly backwardly curved, so that the most posterior is suboval in shape. This segment bears some long setae.

DISCUSSION

The most comprehensive survey of the Solifugae was that of Roewer (1934), which, although an indispensable reference to this arachnid group, is so plagued with inaccuracies and takes such a strict typological approach to systematics that most later workers have experienced severe difficulties in applying Roewer's scheme. Muma (1976) reviewed solifuge families in an attempt to reconcile the situation. His scheme, whilst only tentative, and following Roewer in many aspects, is the most recent 'best guess' at a familial taxonomy, and is followed herein. Some additional information on American families was provided by Maury (1984), and a recent update of Muma's scheme incorporating Maury's changes is given in El-Hannawy (1990).

Some solifuge families are defined by distinct autapomorphies, such as the digging adaptations of the Hexisopodidae, and the hairy claws of Galeodidae, which *Cratosolpuga* lacks. The most useful morphological feature in solifuge taxonomy is the form of the male flagellum. A number of main types can be recognized which can be used to distinguish families. Mesiodorsally placed styliform flagella are found in Solpugidae, Ceromidae, and Daesiidae. Hewitt (1919) discussed the evolutionary development of the flagellum in a survey of the South African solifuges. He regarded the flagellum of daesiids (*Daesia*, *Blossia*, *Melanoblossia*, *Hemiblossia*, *Gluiopsis*), which consists of a membrane with infolded edges which unite at the base to form a cup, to be relatively primitive, and the ceromid flagellum to be derived with respect to that of daesiids. It is movable, styliform and bears a narrow membrane which forms a gutter along the length of the flagellum. The most advanced flagellum in this scheme belongs to Solpugidae, which has a fixed, bulbous base and a long tube (formed by fusion of the edges of the gutter, according to Hewitt) which basally runs forwards along the fixed finger before curving backwards. The American solifuge *Syndaesia* Maury, 1980 bears a tubular flagellum, yet it was placed in Daesiidae by Maury (1980) on account of the movability of the flagellum, the lack of tarsomeres, and other features. The flagellum of *Cratosolpuga*, with its basal bulb, backwardly directed whip and narrow membrane running along its length, is clearly closest in morphology to that of Ceromidae.

The propeltidium of *Cratosolpuga* is wider than long, with distinct lateral lobes that appear to be free anteriorly but fused posteriorly. There is no distinct median divide, as seen in some solifuges. The arci posteriori are raised high above the rear of the propeltidium in the fossil, and the first abdominal tergite is semicircular, with radiating spines around its edge. The eyes are raised on a common tubercle, which bears a pair of prominent, forwardly directed spines. The propeltidium of *Blossia sabulosa* is longer than wide and has a prominent median divide; the first abdominal tergite is bilobed, with radiating setae. The propeltidium of *Ceroma ornatum* is wider than long, the median divide appears only as faint pigmentation; tergite 1 is broadly semicircular. The exterior lobe is anteriorly free and posteriorly attached in both ceromids and daesiids. Overall, the propeltidium and related structures of *Cratosolpuga* more resemble those of ceromids than daesiids.

The presence or absence and, if present, the number of tarsal claws on leg I helps to define families. These vary from none to two. *Cratosolpuga* possibly bears a small leg I tarsal claw.

Solpugidae bear none, Ceromidae two, and Desiidae none or one. The number of segments in the tarsi of legs II to IV is a useful character. The tarsal segment formula (II, III, IV) of *Cratosolpuga* is probably 1, 1, 1, but could be more if the joints are hidden. The formula for Solpugidae is 4, 4, 6/7, for Ceromidae 1, 2, 2, and for Daesiidae 1–2, 1–2, 1–4. The additional tarsal segment in the ceromid *Ceroma ornatum* is short, whilst those of daesiids are rather longer (e.g. Roewer 1934, fig. 274). The paired claws of legs II to IV are situated on a small apotele which in some families, such as Ceromidae and Solifugidae, bears a distinctive pulvillus (= arolium, empodium, onychium, plantium; see Roewer 1934, figs 69–70; Muma 1951, figs 264–270). The tarsal pulvillus of the male of *Ceroma ornatum* studied is large and bifid (see also Roewer 1934, fig. 70), but the female *Ceroma ornatum* studied lacks the pulvillus. The presence of a pulvillus, therefore, is not diagnostic for Ceromidae. Daesiids bear no pulvillus, but in *Blossia sabulosa* there are rows of bristles associated with the claws. The tarsal claws of *Blossia sabulosa* are long, and those of leg IV exceed the length of the telotarsus; in *Ceroma ornatum* the tarsal claws are rather shorter but increase in length from leg I to leg IV. The tarsal claws of *Cratosolpuga* are closer in length to those of the ceromids.

An anteriorly free but posteriorly fused exterior lobe of the propeltidium, as found in *Cratosolpuga*, is characteristic of the families Karschiidae, Solifugidae, Eremobatidae, Ceromidae, Galeodidae and Amacataidae (included in Daesiidae by Maury 1980) (Muma 1976). Other features of the prosomal tergites appear not to be important in solifuge phylogeny.

The cheliceral hands of Ceromidae are distinctly high, dropping at the base of the fixed finger; this feature is found also in *Cratosolpuga*. The pedipalp of *Cratosolpuga* bears prominent spines along its inner edges, presumably to aid in prey capture. The *Ceroma* specimen studied has spines in a similar arrangement but they are rather finer. Similarly, the dense arrangement of thick spines on the propeltidium and chelicerae of *Cratosolpuga* are matched in the modern solifuges studied, but appear rather finer. Possibly the replacement by dense, dark goethite makes them appear more prominent in the fossil than the hyaline spines seen in modern specimens under alcohol.

Leg spination can be of phylogenetic value in solifuges. *Cratosolpuga* bears many spines on the pedipalps. Spinose pedipalps are characteristic of Galeodidae (e.g. Roewer 1934, fig. 315). Ceromids bear long, fine spines in a similar arrangement to *Cratosolpuga* on their pedipalps; some daesiids bear short spines on the pedipalps (e.g. Roewer 1934, fig. 254), whereas others bear long spines (e.g. Roewer 1934, fig. 259); *Blossia sabulosa* has only fine setae.

In conclusion, *Cratosolpuga* is placed in Ceromidae, based on the cheliceral flagellum, the shape of the propeltidium, the eye tubercle, leg spination, and other features. It differs from a typical *Ceroma* male in lacking tarsal pulvilli, and in having only a single tarsal segment on all legs. We consider this placement to be the most appropriate in view of the current state of solifuge systematics, and particularly the lack of a modern, cladistic assessment of familial relationships.

The present-day distribution of solifuges reflects that of deserts, with the exception of Australia and China, where solifuges have yet to be found. This correlation explains the lack of solifuges in most of Brazil and West Africa today, where the dominant habitat is tropical forest. The Chapada do Araripe is situated at about 8° S, and was situated at about the same latitude during mid-Cretaceous times (Smith *et al.* 1981). However, north-east Brazil was located in the centre of a continent in the mid-Cretaceous, and may have experienced a more arid climate than today. Whilst the great diversity and abundance of plant and animal fossils in the Crato Formation attest to a rich biota adjacent to the lake, there is some evidence for a drier climate in the surrounding area. Grimaldi and Maisey (1990) noted the presence of xerophilic arthropods such as Asilidae (Diptera), Myrmeleontidae (Neuroptera) and scorpions as evidence for a drier hinterland to the lake, da Silva (1986) deduced that the lake was saline and landlocked, at least during the later parts of its history, on the evidence of evaporites in the sequence, and Maisey (1990) noted that Gnetales pollen and macrofossils suggested an open, arid environment. The presence of a solifuge adds weight to the hypothesis of an arid palaeoenvironment during deposition of the Crato Formation; though the presence of *Protosolpuga* in Mazon Creek, which represents a tropical forest community, indicates that solifuges have not been confined to arid environments throughout the whole of their geological history.

If Hewitt (1919) is correct in his assumption that the trend in evolution of the male flagellum is from an open cup (Daesiidae) to an elongate, gutter-like form (Ceromidae) to an enclosed tube (Solifugidae), then the phylogenetic relationship (Daesiidae(Ceromidae + Solpugidae)) is implied. Ceromidae are confined to southern Africa at the present day; Daesiidae are known from Africa, southern Europe, the Middle East, and South America. The presence of a ceromid in the Cretaceous means that the split between the sister lineages Daesiidae and (Ceromidae + Solpugidae) had occurred before this time. The disjunct distribution of daesiids at the present day suggests an earlier widespread occurrence of that family. The origin of the ceromid + solifuge clade may have occurred during the initial rifting events of Pangaea to form the proto-Atlantic ocean in the Cretaceous, since fragmented land masses in the rifting zone would have led to speciation events. Later, changes in the climate adjacent to the new ocean could have caused extinction of solifuges from the areas now occupied by Brazil and West Africa. The predominantly African distribution of Solpugidae at the present day (none is known from South America), concurs with the hypothesis of the development of this family from Ceromidae, or a common ancestor, after the rifting event.

SYSTEMATIC PALAEONTOLOGY

Order SOLIFUGAE Sundevall, 1823

Genus PROTOSOLPUGA Petrunkevitch, 1913

Remarks. The diagnosis presented by Petrunkevitch (1913) is partly incorrect and quite inadequate for separating this animal from any other solifuge genus. The only 'feature' distinguishing this fossil from any other solifuge is the fact that it is Carboniferous; all other known solifuges are Cretaceous or younger. A new family, Protosolpugidae, was erected for this specimen by Petrunkevitch (1953) without discussion. Two years later, he placed it provisionally in Galeodidae Pocock, 1897, an assignment which was 'entirely arbitrary and was motivated by the fact that this family has a wide Old-World distribution' (Petrunkevitch 1955, p. P154). Since it cannot be supported by any real evidence, we prefer not to assign the fossil to any modern solifuge family.

Protosolpuga carbonaria Petrunkevitch, 1913

Plate 1, figures 1–2; Text-figure 2

- 1913 *Protosolpuga carbonaria* Petrunkevitch, p. 74, fig. 40.
- 1949 *Protosolpuga carbonaria* Petrunkevitch, p. 292.
- 1953 *Protosolpuga carbonaria* Petrunkevitch, p. 112.
- 1955 *Protosolpuga carbonaria* Petrunkevitch, p. P155, fig. 112,3.

Material. Holotype and only known specimen, 00155/B1336 in the Peabody Museum, Yale University, New Haven, Connecticut. The specimen is from the Late Carboniferous (Westphalian D) Francis Creek Shale of Mazon Creek, Illinois.

Remarks. See remarks above for the genus, of which this is the type and only known specimen.

Description. See *Morphological interpretation*, above.

Family CEROMIDAE Roewer, 1934

Remarks. The cheliceral flagellum of the Cretaceous is clearly ceromid in character, as are many other features, such as the shape of the propeltidium, the eye tubercle, leg spination, etc. The fossil genus differs from a typical *Ceroma* male in lacking tarsal pulvilli (though this is not a diagnostic character), and in having only a single tarsal segment on all legs.

Genus *CRATOSOLPUGA* Selden gen. nov.

Derivation of name. From the Crato Formation, the stratum in which the fossil was discovered, and *Solpuga*, a typical genus of Solifugae.

Type species. *Cratosolpuga wunderlichi* Selden, sp. nov., by monotypy.

Diagnosis. Male cheliceral flagellum attached to dorsomedial side of chelicera near base of fixed finger, consisting of globose base and styliform whip extending directly backwards to base of chelicera, stiff membrane partly enclosing flagellum base and running length of flagellum forming a narrow gutter. Single tarsomere on all legs.

Cratosolpuga wunderlichi gen. et sp. nov.

Plate 1, figures 3–4; Text-figures 4–6.

Derivation of name. In honour of Jörg Wunderlich, who recognized the importance of the holotype specimen and sent it to PAS for study.

Material. Holotype specimen, part only, No. Sol 1 is deposited in the collection of J. Wunderlich, Straubenhardt, Germany. Additional (presumed juvenile) specimen (not to be regarded as a paratype), part only, No. SMNK 1268 PAL in the Staatliche Museum für Naturkunde, Karlsruhe, Germany. Both are from the Crato Formation, Lower Cretaceous (Aptian) of the Chapada do Araripe, Ceará Province, north-eastern Brazil.

Diagnosis. As for the genus.

Description of holotype. Medium-sized solifuge (Text-fig. 5). Propeltidium anterior margin nearly straight mesially, curving gently backwards towards lateral, exterior lobes separated from propeltidium anteriorly, fused to propeltidium posteriorly. Anterior margin a definite ridge which extends to point where exterior lobe is fused. Posterior margin of propeltidium approximately semicircular. Total width of propeltidium (including exterior lobes) 3.3 mm, length 1.9 mm. Eyes at anterior edge of propeltidium, each on a radially ridged, raised lobe, these lobes both situated on a common eye tubercle; lens diameters about 0.23 mm and about a diameter apart, rugose cuticle between and around eye tubercles. One pair of short spines emerges from between the eyes and points anterolaterally; another pair occurs beneath these. Propeltidium thickly clothed with spines. Exterior lobe raised into pyramidal shape (broken on right side). Median plagula of propeltidium not distinct from anterior arci. Posterior arci of parapeltidium transverse. Junction between anterior and posterior arci of parapeltidium forms prominent transverse ridges. Parapeltidium thickly clothed with spines. Mesopeltidium a distinct semicircular tergite, deeply concave with raised anteromesial area and raised rim; a row of large spines radiate from the tergite around its rim. Metapeltidium and dorsal opisthosoma not preserved. Only a few, scattered hairs mark the impression of the ventral opisthosoma between the femora of legs IV.

Chelicerae 3.3 mm long, basal body 2.3 mm long, globose, pyriform, as high as, or higher than, propeltidium (but somewhat crushed in fossil). Thickly clothed with thick spines; two very large spines present on posterolateral dorsal surface, directed backwards over anterior border of propeltidium. Long, forwardly directed spines on anterior part of body. Long, fine setae present near base of flagellum. Fixed finger incomplete. Movable finger appears slightly lateral to fixed finger, with mesially curved tip. Flagellum situated on dorsal surface of chelicera at base of fixed finger. Flagellum a backwardly directed, styliform structure, with globose base. Narrow membrane at first partially enclosing base, then running the length of flagellum on the exterior side. Membrane forms a gutter-like structure, the membrane edge distally dominating the formation of the acicular flagellar tip.

Pedipalps robust, forwardly directed, with many long spines on mesial surfaces of trochanter, femur, patella and tibia. Podomeres thickly clothed with fine spines, long trichobothria also present. Trochanter appears as triangular feature adjacent to chelicera; two spines project forward. Femur with row of about six large spines on mesial surface, with smaller spines between, the larger ones increase in length (longest exceeding thickness of podomere) from the base to about two-thirds of podomere length, then decrease. Distal joint bears large triangular area of leathery cuticle on mesial side. At least four prominent spine bases occur in distal half of

dorsal surface. Right femur has some cuticle broken away from the dorsal surface, revealing a tendon. Patella bears about six large spines on the mesial surface, which increase in length towards middle of podomere (longest exceeding thickness of podomere), with shorter spines between. Two prominent spine bases occur at mid-length on the dorsal surface. Large area of leathery cuticle stretches across mesial side of pa-ti joint. Tibia bears a row of five (possibly six) large spines alternating with shorter spines, themselves with smaller spines between, and there is a thick clothing of long, fine hairs. At least two large spine bases are present on the dorsal surface at about mid-length. Distal tibia joint is distinct; little constriction in width of the tibia at the joint. Marked edge to end of tibia at inner side of ti-ta joint, outer side shows wrinkled cuticle. Tarsus short, somewhat bulbous, broader than tibia distally, and probably movable. Tarsus bears many thin spines, and a large sucker at the tip. Podomere lengths (in mm): tr 0.8; fe 5.2; pa 5.1; ti 3.5; ta 1.0.

Leg I thickly clothed in short and long, fine bristles but no thick spines. Short trochanter bears at least two spines dorsally, and short first femur distinctly narrower dorsally than elsewhere. Second femur long, tibia slightly longer than second femur, basitarsus shorter than these podomeres. Telotarsus about half the length of basitarsus and bearing stout bristle(s) at tip which may include claw(s). Podomere lengths (in mm): tr $\geq$ 0.5; fe 1.2 (max.); pa 4.1, ti 4.2; ta1 2.9; ta2 1.5.

Leg II stouter than leg I but is shortest of all legs. Clothed in many fine hairs or bristles (as evidenced by the density of follicles seen on the dorsal surface) and bearing some stout (but where preserved rather short) spines. Trochanter presented with its distal joint uppermost in the fossil, and the short first femur is similarly disposed, so it is impossible to provide meaningful lengths for podomeres. Trochanter bears at least two spines dorsally. Patella relatively short, and tibia about the same length. Patella bears two prominent spine bases at one-third and two-thirds the length of the podomere on its dorsal side, distalmost is the larger. Smaller spine bases scattered across the dorsal surface. Prominent articulations at the proximal pa joint (dorsal) and distal pa joint (anterodorsal); latter joint shows an area of leathery cuticle across the joint on the anterior side. Slightly curved spine on the anterior side of the distal joint. Basitarsus slightly shorter than the preceding two podomeres and shows articulation dorsally at distal joint. A row of five stout, gently distally curved, spines occurs on dorsal surface, second and fourth spines slightly removed towards the posterior surface. Spine opposite fourth dorsal spine on anterior surface. Telotarsus approximately half length of basitarsus. On both sides, telotarsus is bent posteriorly; it bears bristles and paired spines ventrally. Telotarsus probably a single segment, but if composed of tarsomeres then a maximum of four is present. Pairs of long, curved, naked claws present; each bearing a joint near the tip. Podomere lengths (in mm): pa 2.8; ti 2.5; ta1 1.9; ta2 1.1 (excluding claws; claws c. 0.8).

Leg III longer than leg II, and as stout, but shorter than leg I. Thickly clothed with long bristles and short and long spines. Trochanter appears slightly larger than that of leg III, but is not well enough preserved to estimate quantitative size. Basifemur short, and narrower dorsally than ventrally. Dorsal side bears large spines (one is present on the left side, at least one more is apparent from preserved spine bases). Femora are bisected on both sides by a crack in the specimen. Distal joint of patella bears an articulation anterodorsally and an area of leathery cuticle anterior to this. Tibia shorter than patella and less stout. It bears some long spines anteriorly and one large spine base medially on the dorsal surface. Basitarsus shorter than tibia; it is thickly clothed with bristles and bears rows of spines. Telotarsus shorter than basitarsus, and similarly clothed with bristles and pairs of spines. Telotarsus appears to be a single segment, but if tarsomeres present then a maximum of four. Two long, curved, naked claws are present, each bearing a joint near the tip. Podomere lengths (in mm): fe1 0.7; fe2+pa c. 4.9; ti 3.8; ta1 2.5; ta2 1.4 (excluding claws; claws 0.8).

Leg IV the longest. Thickly clothed with hairs, long bristles, and spines. Proximal podomeres poorly preserved, but remnants of two racquet organs (malleoli) preserved on the right side. Judging from their position, these belong to the trochanter and basifemur (distal). Only a small part of the telofemur is preserved on the left side, very short dorsally. Patella large; only some ventral bristles are preserved on the right side but left one fully preserved. It bears long, thin, slightly curved spines, in addition to fine bristles, apparently on all surfaces. Distal joint shows an articulation on the side which is now dorsal; leathery cuticle present anterior to this. Tibia is about as long as patella but thinner; bears short spines and bristles. Basitarsus shorter than tibia but similarly clothed in fine spines, hairs, and bristles. Telotarsus bears fine bristles, long hairs, and paired spines, and appears as a single, curved segment; if tarsomeres present then maximally seven. Pair of naked, curved claws present on a small apotele; each claw has a joint near the tip. Podomere lengths (in mm): pa 5.3; ti 5.0; ta1 3.7; ta2 2.2 (excluding claws; claws 1.0).

Description of additional specimen. Small (5.8 mm long including chelicerae) specimen, presumed to be juvenile, and almost all parts of body preserved (Text-fig. 3). Specimen shows predominantly ventral structures seen from the dorsal (internal) aspect. Free fingers of chelicerae expand slightly anteriorly to mid-length, then taper

to a slightly curved point. A fragment of fixed finger overlies each movable finger. Pedipalp coxae large, trapezoidal, straight mesial edges run parallel in midline, parallel anterior and posterior edges subtend an angle of 40° from the midline. Leg I coxa parallel to pedipalp coxa, but without straight mesial edge. Coxae I do not meet mesially, but are separated by a small triangular sclerite with apex anterior. Coxae II and III transverse. Coxae IV poorly preserved. Pedipalp patella with two, parallel rows of about four long spines, tibia with more, irregularly arranged long spines. Richly clothed in long, fine setae and some trichobothria. Short telotarsus. Approximate podomere lengths (in mm): fe 1.4, ti 1.4; ta1 1.4; ta2 0.5. Leg I thin, mostly obscured by pedipalp. Richly clothed in long, fine setae and some trichobothria. Leg II short, at least seven short spines on basitarsus and telotarsus, telotarsus thickly clothed with setae, claws not seen. Approximate podomere lengths (in mm): fe 0.4; pa 0.6; ti 0.6; ta1 0.7; ta2 0.5. Leg III longer than leg II, two large spines on distal end of tibia, tarsal claws not seen. Approximate podomere lengths (in mm): fe2 0.4; pa 1.0; ti 0.9; ta1 0.9; ta2 0.6. Leg IV collapsed proximally, proximal podomeres poorly preserved, malleoli not seen. Proximal and distal pairs of long spines on basitarsus, at least one pair of long spines on telotarsus, claws not seen. Telotarsus thickly clothed with setae, long trichobothrium on tibia. Approximate podomere lengths (in mm): ti 0.8; ta1 0.6; ta2 1.0. Ten abdominal segments. Second bilobed, third to sixth subrectangular, more posterior become increasingly backwardly curved, so that tenth is suboval. Tenth (anal) segment bears long setae.

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A TRIGONOTARBID ARACHNID FROM THE UPPER SILURIAN OF SHROPSHIRE

by JASON A. DUNLOP

ABSTRACT. A trigonotarbid (Arachnida: Trigonotarbida) from the oldest known terrestrial ecosystem (Silurian, Přídolí Series) of Ludford Lane, Shropshire, UK is described as *Eotarbus jerami* gen. et sp. nov., and is the earliest known non-scorpion arachnid. This specimen predates Rhynie Chert and Gilboa trigonotarbids which show more plesiomorphic characters, and is similar to some Early Devonian trigonotarbids from Alken an der Mosel and other German localities of similar age. *Eotarbus jerami* is too poorly preserved to be assigned unequivocally to a family, but most closely resembles the Trigonotarbidae. *Eotarbus* is interpreted as a plesion and is probably a sister group to all trigonotarbids with triangular carapaces lacking lateral eyes.

TRIGONOTARBIDS are a group of spider-like arachnids which range from the late Silurian (Jeram *et al.* 1990) to the early Permian (Müller 1957), and are one of the most diverse and abundant groups of Palaeozoic terrestrial arachnids. Recent work (Shear and Selden 1986; Shear *et al.* 1987; Dunlop 1994*a*, 1994*b*) placed the trigonotarbids in the arachnid taxon Tetrapulmonata Shultz, 1990, as the plesiomorphic sister group of all the living tetrapulmonates (Araneae, Amblypygi, Uropygi and Schizomida) (Shear *et al.* 1987). Until recently, the oldest known examples of trigonotarbids were the exceptionally preserved Lower Devonian (Pragian) Rhynie Chert fauna (e.g. Hirst 1923; Shear *et al.* 1987). Jeram *et al.* (1990) made an initial report of some older terrestrial fossils macerated from Silurian (Přídolí Series) sediments from Ludford Lane, Shropshire. Among the arthropod and plant fragments recovered was a single specimen of an unnamed trigonotarbid arachnid (Jeram *et al.* 1990, fig. 1), and this is described herein, and compared with Devonian and Carboniferous trigonotarbids.

GEOLOGICAL SETTING

The specimen was recovered from an organic-rich horizon within the Ludlow Bone Bed Member of the Downton Castle Sandstone Formation, from Ludford Lane, Ludlow, Shropshire, UK. The precise horizon is unrecorded, but subsequent investigations suggested that the richest organic deposits are 1.6 m above the basal bone bed of the Ludlow Bone Bed Member, within the Platyschisma Shale Member (Manning 1993). The Ludford Lane sequence has been described by Bassett *et al.* (1982), and is interpreted as a near-shore deposit into which terrestrial plant and animal material was transported and then reworked during severe storms (Manning 1993; Manning and Dunlop 1995). It contains an assemblage of marine and terrestrial fossils. The former are predominantly eurypterids (Manning 1993), but also include aquatic scorpions, scoliodonts, thelodont denticles and, rarely, conodonts. The latter comprise vascular land plants, such as *Cooksonia* (Edwards *et al.* 1992), centipedes (Jeram *et al.* 1990), the arthropleurid *Eoarthropleura* (Shear and Selden 1995) and probable terrestrial scorpions (Manning (1993); A. Jeram, pers. comm.) Further arthropod material from this locality awaits description.

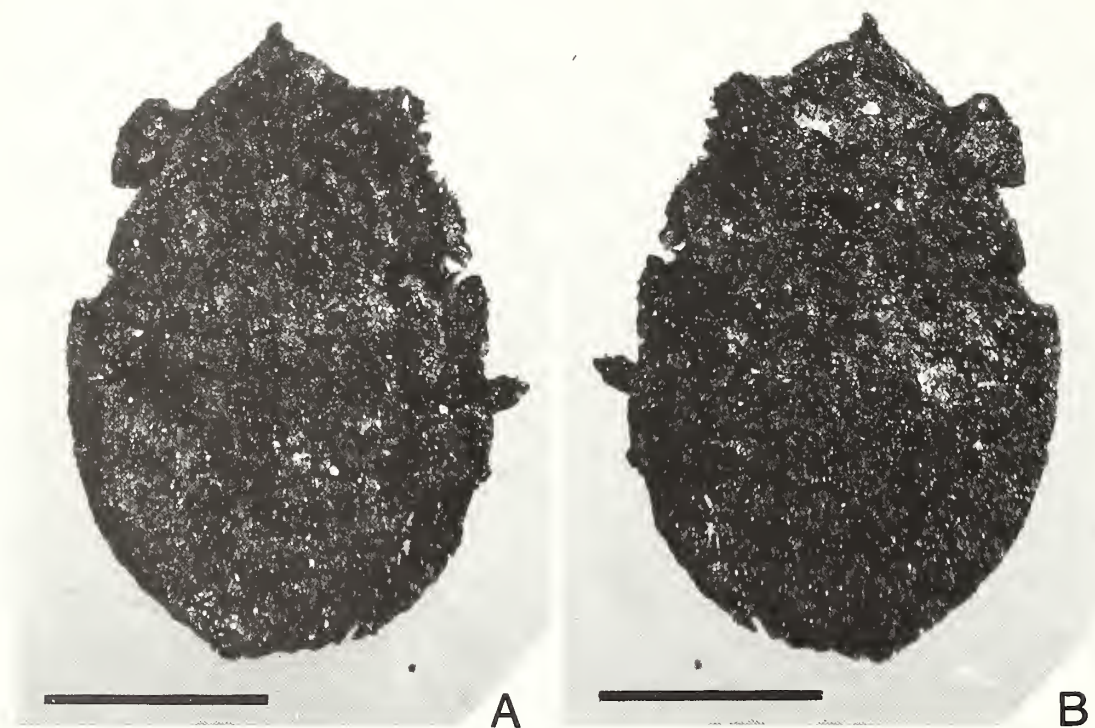
The Ludford Lane arthropod fossils are preserved as fragile fragments of cuticle, or, more rarely, nearly complete animals, as is the case with this trigonotarbid. The specimen is carbonized, which obscures morphological details of the cuticle, such as can be seen in the better preserved Gilboa trigonotarbids (Shear *et al.* 1987), and is compressed, but morphological features can be seen under low angle lighting.

MATERIALS AND METHODS

The material was originally prepared by A. Jeram using palaeobotanical hydrofluoric acid (HF) maceration techniques following methods described by Shear *et al.* (1987) and Manning (1993). The slide-mounted specimen, Ulster Museum K 25850, was examined and photographed under a binocular microscope with very low angle lighting to bring out the faint surface relief. Drawings were prepared using a *camera lucida*. Specimens of the trigonotarbids *Palaeocharinus* sp., from the Early Devonian (Pragian) of the Rhynie Chert, Aberdeenshire, and *Trigonotarbys johnsoni*, from the Upper Carboniferous of Coseley, West Midlands in the collections of the Natural History Museum, were examined in conjunction with the literature for comparative purposes.

MORPHOLOGICAL INTERPRETATION

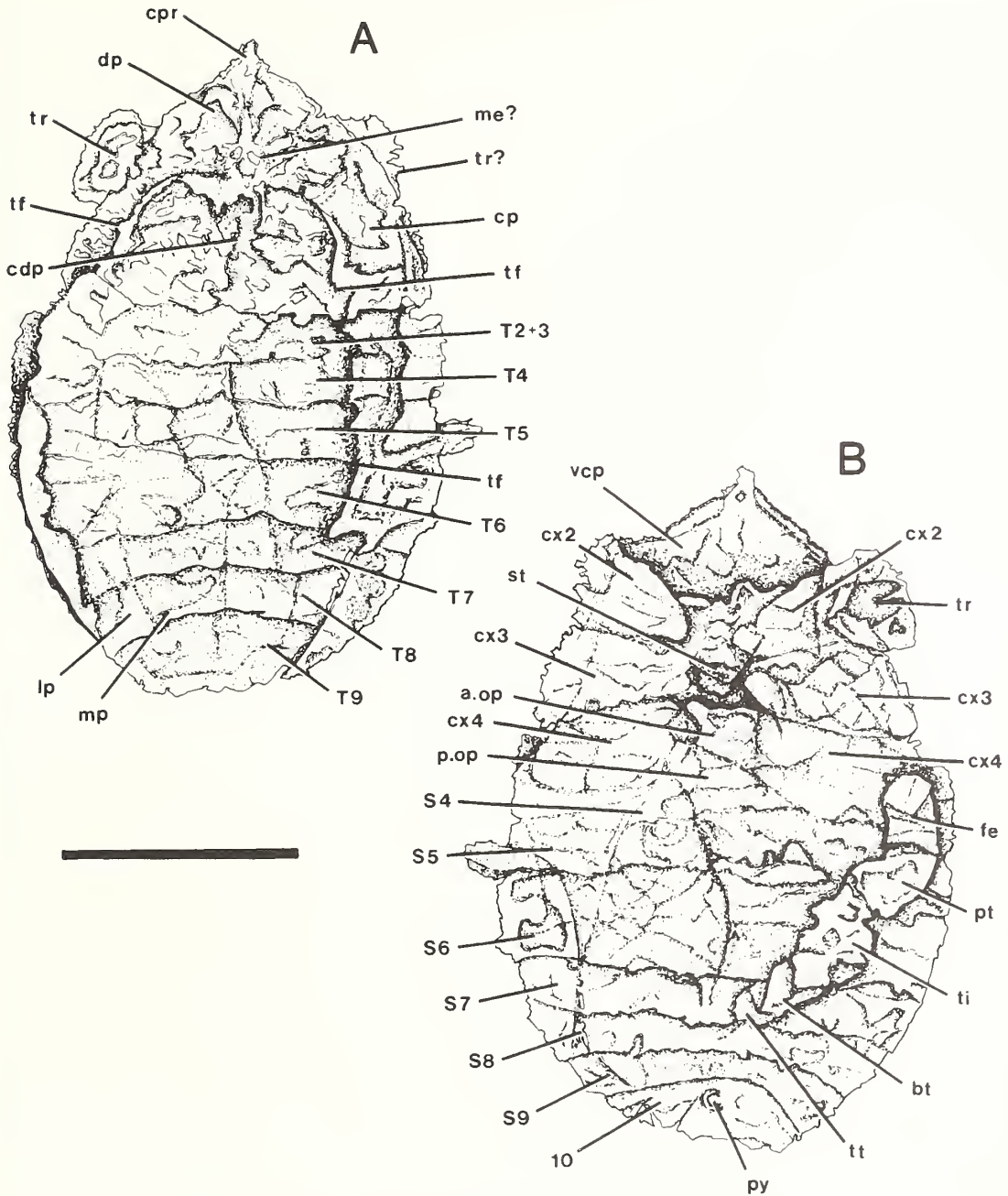
The carbonized preservation of this specimen makes interpretation difficult, but its overall body shape, with a triangular prosoma and rounded opisthosoma, and its division of the opisthosomal tergites into median and lateral plates shows that it is a trigonotarbid (Text-figs 1–2).



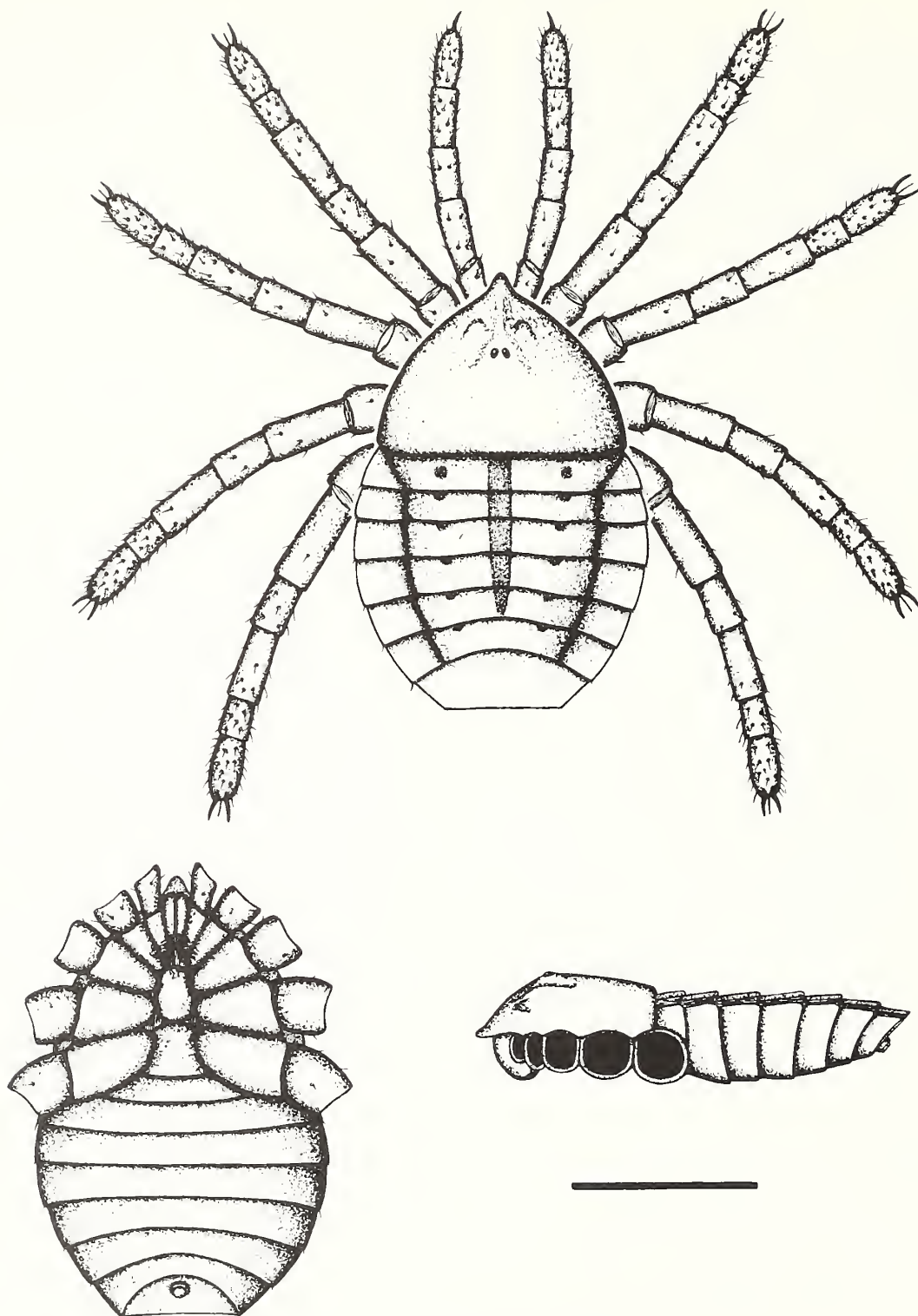
TEXT-FIG. 1. *Eotarbys jerami* gen. et sp. nov. Silurian (Pridoli), Ludford Lane, Shropshire. Ulster Museum No. K 25850. A, dorsal surface. B, ventral surface. Scale bar represents 0.5 mm. Photographs courtesy of Dr A. Jeram.

Carapace

The carapace is broadly triangular, with a slight anterior projection and a straight posterior margin. It is folded and pitted, but shows some original surface detail. It appears raised close to the assumed



TEXT-FIG. 2. *Camera lucida* drawing of the specimen shown in Text-figure 1. A, dorsal surface, B, ventral surface, a.op = anterior operculum; bt = basitarsus; cdp = central (?taphonomic) depression of carapace; cp = carapace; cpr = anterior projection of carapace; cx = coxa, with number; dp = anterior depressions of carapace; fe = femur; lp = lateral plate; me? = probable position of median eyes; mp = median plate; p.op = posterior operculum; pt = patella; py = pygidium; S = sternite, with number; st = sternum; T = tergite, with number; tf = taphonomic folding of cuticle; ti = tibia; tr = trochanter; tt = telotarsus; vcp = ventral surface of carapace. See text for details. Scale bar represents 0.5 mm.



TEXT-FIG. 3. For caption see opposite.

position of the eyes and the two notches anterior to these 'eyes' appear to be genuine, rather than taphonomic features, since they are approximately symmetrical about the midline of the animal (Text-fig. 2). There are two strong lateral folds on the carapace (Text-fig. 2), but these are not in the same position on each side, and the stronger right hand fold continues onto the opisthosoma. This suggests that the folds are principally taphonomic, perhaps caused by crushing of the central region (Text-fig. 2). This interpretation is preferred over one in which the folds indicate a raised median region to the carapace, which might be expected to produce strong, symmetrical folds on either side of the midline. The carapace shows some evidence for a pair of median eyes (Text-fig. 2), but none for lateral eye tubercles, such as those seen on the carapaces of the palaeocharinid trigonotarbid from the Rhynie Chert and Gilboa (Shear *et al.* 1987). If lateral eye tubercles were present in life, it might be expected that crushed remnants of these could be detected as paired, slightly raised structures on the anterior half of the carapace of this specimen, even if individual lenses could not be resolved. I believe it is more parsimonious, though admittedly equivocal, to interpret the carapace as a moderately high, dorsally flattened structure, slightly raised around the apparent position of the median eyes than to reconstruct it with a more complex morphology, the evidence for which would be equally equivocal.

Appendages

The preserved coxae radiate around the sternum in a typical trigonotarbid pattern. Two of the coxal pairs are clearly evident and are labelled as coxae 2 and 3, but the pair interpreted as coxae 4 are not distinct (Text-fig. 2) and may have been compressed against the opisthosoma. The alternative interpretation would be that the coxa labelled 3 is in fact coxa 4, and this would indicate a situation different from that in other trigonotarbid, where coxae 4 often attach just behind the sternum (Dunlop 1994a) rather than against its lateral sides. Also, the coxa labelled 3 is directed laterally, whereas in most arachnids coxa 4 is directed posterolaterally (and coxa 3 is directed laterally) so that leg 4 is directed backwards to improve the stability of the animal during walking. The interpretation shown in Text-Figures 2–3 is further supported by the fact that only the leg 1 coxae, the palpal coxae and the chelicerae have to be fitted into the space beneath the carapace in which the chelicerae and coxae are not preserved (Text-fig. 2). If the coxa interpreted as coxa 3 is in fact coxa 4, then two leg coxae, the palpal coxae and the chelicerae would have to be squeezed into this space, which appears too small to accommodate the basal podomeres of eight additional appendages. I therefore favour the interpretation shown in Text-figures 2–3, although the imperfect preservation leaves this open to question. The coxo-sternal region and prosoma-opisthosoma junction of the better preserved Rhynie Chert material will be investigated more fully in a subsequent publication.

The entire limb series is not preserved in this specimen, but an incomplete leg is preserved bent across the opisthosoma, comprising a partial femur, the patella, tibia, basitarsus and a partial telotarsus. This leg may represent leg 3 since the incomplete femur rests over what is interpreted as the leg 4 coxa and would probably have extended back to about the position of the leg 3 coxa, though it could conceivably be a displaced leg 4. Knowledge of the podomere proportions of the femur and telotarsus in other early trigonotarbid (e.g. Hirst 1923; Shear *et al.* 1987) allows its total length to be estimated at a little over 1 mm. In most trigonotarbid all the walking legs are approximately the same length, with legs 1 and 4 being a little longer (Dunlop 1994a). On this basis, a tentative reconstruction of the limb series of this animal can be made (Text-fig. 3). The size of the pedipalps in this reconstruction is hypothetical, and based on analogies with the Rhynie Chert material (Hirst 1923).

TEXT-FIG. 3. Reconstruction of *Eotarbus jerami* gen. et sp. nov. Majority of legs, part of coxosternal region and position of opisthosomal heart and muscle apodemes hypothetical, and reconstructed in comparison with more complete trigonotarbid from the Rhynie Chert, and Recent arachnids. Scale bar represents 0.5 mm.

Opisthosoma

The dorsal opisthosoma shows clear transverse divisions under low angle lighting which are assumed to represent tergite boundaries. The specimen is interpreted as showing seven visible dorsal tergites (Text-fig. 2). In comparison with the opisthosoma in the Rhynie Chert and Gilboa trigonotarbid (Shear *et al.* 1987), these are assumed to represent a fused diplotergite 2+3 (tergite 1 being a modified locking ridge tucked under the carapace in palaeocharinids (Shear *et al.* 1987)), and then sequentially tergites 4–9. The only concern with this interpretation is tergite 6 (Text-fig. 2) which seems rather long on the left-hand side, and possibly even subdivided here which would suggest an 'extra' tergite. If this were true then tergites 2 and 3 would be interpreted as unfused, with no diplotergite, giving eight dorsally visible tergites. The opisthosoma posterior to tergite 5 has rotated slightly anticlockwise which confuses the morphology of this region. Subsegmentation of tergite 6 cannot be traced all the way across the opisthosoma, and so the interpretation shown in Text-figures 2–3 is preferred, with reservations. The pattern of segmentation shown in Text-figure 2 with tergites 2 and 3 fused into a diplotergite seems to characterize the majority of trigonotarbid (Dunlop 1994*a*), the exception being the rather derived Carboniferous family Eophrynidae (Dunlop 1994*b*). The left side of the opisthosoma shows, faintly, the division into median and lateral plates which characterizes trigonotarbid tergites. A major fold on the right hand side (Text-fig. 2) may be associated with the division into lateral plates, but could be taphonomic since it continues on to the carapace as discussed above. There is no obvious tuberculation and/or spination on the opisthosoma, unlike in some geologically younger trigonotarbid (Dunlop 1994*b*). Overall, the dorsal opisthosoma seems to follow the pattern of tergites 2+3 fused and tergite 9 not divided into median and lateral tergites, which is also seen in the Rhynie Chert palaeocharinids and all other Devonian trigonotarbid studied by the author (Dunlop 1994*a*).

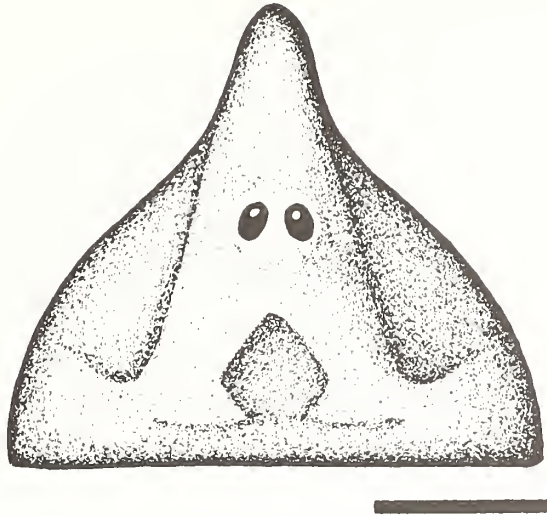
The ventral opisthosoma shows segmentation, but not as distinctly as the dorsal surface, so the reconstruction of segmentation in Text-figures 2–3 is partly hypothetical. Posteriorly, a pygidium (segments 11 and 12, not 10 and 11 as reported by Shear *et al.* (1987)) can be made out surrounded by a plate interpreted as segment 10, not divided into tergites and sternites, with sternite 9 (which connects to the corresponding tergite 9) surrounding this segment. Trigonotarbid appear to have lost sternite 1 (Dunlop 1994*a*) and in comparison with studies of uropygids (Shultz 1993) the next two sclerites ('sternites' 2 and 3 in trigonotarbid) are interpreted not as true sternites, but as highly modified appendages bearing the respiratory organs. Following Shultz's (1993) terminology, these are termed the anterior and posterior operculae respectively, and their probable position is noted on Text-figure 2. This pattern of ventral opisthosomal segmentation in trigonotarbid differs from that given in previous accounts (e.g. Petrunkevitch 1949; Shear *et al.* 1987) in the recognition of operculae, and is being explored more fully by the author in the much better preserved Rhynie Chert material.

The reconstruction (Text-fig. 3) shows the suggested appearance of *E. jerami* in life based on the above interpretation and draws partly on comparison with the exceptionally preserved Rhynie Chert material for the distribution of chelicerae, setae, muscle apodemes, etc. This animal was probably a predator on some of the other early terrestrial arthropods in the Ludford Lane ecosystem.

PHYLOGENETIC RELATIONSHIPS

The poor preservation of the Ludford Lane trigonotarbid and the equivocal status of many of its morphological details makes its phylogenetic placement difficult. Its small size and weak sclerotization are reminiscent of the Devonian family Palaeocharinidae Hirst, 1923, redefined by Shear *et al.* (1987) as trigonotarbid retaining lateral eyes. There is nothing to support the presence of lateral eyes in *Eotarbus*, though the evidence is not conclusive for or against their presence. All other trigonotarbid with a triangular carapace lack lateral eyes (Dunlop 1994*a*). The best preserved Rhynie Chert material shows these palaeocharinids to have a box-like carapace with subparallel lateral sides, distinct oval lateral eye tubercles and an anteriorly projecting clypeus (e.g. Hirst 1923,

TEXT-FIG. 4. Reconstruction of the carapace of *Trigonotarbus johnsoni*, based on Natural History Museum no. I. 15897, showing the prominent median ridge which differentiates it from *Eotarbus jerami*. Scale bar represents 1 mm.



pls 12–14; Dunlop 1994a). This is significantly different from the triangular carapace of *Eotarbus* and on these grounds of carapace morphology I believe that *Eotarbus* should not be referred to the Palaeocharinidae.

The triangular carapace and rounded body of the Ludford Lane trigonotarbid are most reminiscent of the family Trigonotarbiidae Petrunkevitch, 1949. Specimens of *Trigonotarbus johnsoni* from the British Middle Coal Measures were examined, and considering this, and other material referred to the Trigonotarbiidae, a revision of this family is required. Petrunkevitch (1949, 1953) diagnosed it as having eight opisthosomal segments. However, Petrunkevitch's morphological interpretations of fossil arachnids and their segmentation have been questioned (e.g. Shear *et al.* 1987; Selden 1993). Examination of the type material of *T. johnsoni* (unpublished observations) suggests errors in Petrunkevitch's description of this specimen, making his diagnosis of the family unreliable.

The Ludford Lane specimen appears to differ from *T. johnsoni* in one important character. The carapace of the latter has a raised median ridge bearing a single eye tubercle, widening posteriorly and then curving back on itself on each side, to merge with the rest of the carapace, with a diamond-shaped depression in the median ridge posterior to the eyes (Text-fig. 4). This morphology may represent a better diagnostic character for the Trigonotarbiidae. The carapace of *Eotarbus* shows no evidence of such a strong median ridge and is interpreted as being a relatively flat structure (Text-fig. 3), though the evidence for this is equivocal. I am reluctant to refer *Eotarbus* to Trigonotarbiidae since there are apparent differences in carapace morphology between *Eotarbus* and *Trigonotarbus* and the diagnostic characters of Trigonotarbiidae are poorly constrained. *Eotarbus* might represent a new, monotypic, family, but owing to its poor preservation and equivocal diagnostic characters I prefer to leave its familial status open and regard *Eotarbus* as a plesion as discussed below.

Devonian trigonotarbids

In addition to the Palaeocharinidae discussed above, there are four other Devonian trigonotarbid species. Of these, *Alkenia mirabilis* from the Lower Devonian (Emsian) of Alken an der Mosel, Germany, is a relatively large, tuberculated form with an oval carapace lacking lateral eyes (Störmér 1970; Shear *et al.* 1987) which does not appear to be closely related to *Eotarbus*. Of the other three, all referred to the Trigonotarbiidae (see above), *Archaeomartus levis* from the Emsian of Alken an der Mosel and the Rheinisches Schiefergebirge (Störmér 1970; Brauckmann 1987) and *Trigonotarbus stoerméri* from the Rheinisches Schiefergebirge (Schultka 1991) both show a triangular prosoma and rounded opisthosoma and are thus superficially similar to *Eotarbus*.

Archaeomartus tuberculatus, also from Alken an der Mosel, is known only from an isolated opisthosoma (Störmer 1970). Brauckmann's (1987, pl. 2) specimen of *A. levis* represents a ventral opisthosoma and the internal surface of the carapace, which does not show a strong median lobe as in *T. johnsoni*. Schultka's *T. stoermeri* is poorly reconstructed (Schultka 1991, fig. 1) and he interpreted many ventral structures as dorsal, but figured a triangular carapace (Schultka 1991, fig. 11) with a raised median region. This carapace is therefore reminiscent of that of *T. johnsoni* (Text-fig. 4) and supports Schultka's placement of *T. stoermeri* in the Trigonotarbitidae. Because the diagnostic characters of Trigonotarbitidae are equivocal, the position of all the Devonian taxa requires revision. Study of the opisthosomal segmentation of taxa referred to this family may further refine the phylogeny of this group.

Trigonotarbitid phylogeny

Shear *et al.* (1987) regarded the presence of lateral eyes as representing the plesiomorphic state in both trigonotarbitids and arachnids in general. *Eotarbus*, apparently lacking lateral eyes, therefore appears to be more derived than the younger palaeocharinids. Outgroup comparison with eurypterids, most of which have a rectangular carapace bearing a pair of lateral eye tubercles (carapaces similar to those of palaeocharinids in some respects), also suggests that a triangular carapace is an apomorphic character. Although the oldest trigonotarbitid (and the oldest tetrapulmonate arachnid), *Eotarbus jerami*, apparently lacking lateral eye tubercles, appears not to be the most 'primitive' trigonotarbitid; the younger Rhynie Chert trigonotarbitids show more plesiomorphic characters (Dunlop 1994a). *Eotarbus* provides evidence for an early split of the Trigonotarbitida into two major lineages: an earlier one retaining more plesiomorphic characters such as lateral eyes, i.e. the Palaeocharinidae (and perhaps also the Anthracomartidae and Anthracosironidae (Dunlop 1994a)) and a more derived one, with triangular and subtriangular carapaces, in which the lateral eyes are lost, i.e. all other families (see below). This split must therefore have occurred prior to the late Silurian and predicts the presence of even older palaeocharinids. Whether these trigonotarbitids were aquatic or terrestrial is unknown. *Eotarbus* cannot be referred confidently to any existing family and shows no strong autapomorphies. If the carapace could be demonstrated unequivocally to lack a median lobe this might represent a diagnostic character, but outgroup comparison with eurypterids, which also lack a median lobe, suggests this would be a plesiomorphic character rather than an apomorphic one, and therefore a poor diagnostic character. On these grounds, I believe that *Eotarbus* should be regarded as a plesion. *Eotarbus* may represent a sister group for all triangular- and subtriangular-carapaced trigonotarbitids lacking lateral eyes, i.e. the Trigonotarbitidae, Lissomartidae, Dunlop 1995, Aphantomartidae and Eophrynidae.

SYSTEMATIC PALAEONTOLOGY

Class ARACHNIDA Lamarck, 1801

TETRAPULMONATA Shultz, 1990

Order TRIGONOTARBIDA Petrunkevitch, 1949

Emended diagnosis. Tetrapulmonate arachnids with 12 opisthosomal somites. Tergite 1 forming a ridge associated with a locking device with the prosoma, reduced in some families. Tergites 2–8 (2–9 in some) divided into median and lateral plates, tergites 2–3 fused in some families, tergites 4–9 not fused. Sternite 1 absent. Terminal three segments not divided into tergites and sternites, terminal two segments forming a pygidium. Pedipalps and walking legs pediform. Chelicerae two segmented and of the clasp-knife type.

Remarks. The above definition differs from that given by Shear *et al.* (1987) in recognizing a 12-segmented opisthosoma and the lack of fusion among tergites 4–9 which is seen in ricinuleids. Ricinuleids also have tergites divided into median and lateral plates and a prosoma-opisthosoma

locking device. The arachnid order Trigonotarbida was erected by Petrunkevitch (1949) from material originally placed in the order Anthracomartida. This division into two orders is almost certainly invalid and Anthracomartida should be synonymized with a revised Trigonotarbida (Dunlop 1994a). A formal account of this synonymy is currently in preparation.

Plesion (Genus) *EOTARBUS* gen. nov.

Derivation of name. From the Latin, *Eo*, dawn, and the suffix, *tarbus*, fear.

Type and only known species. *Eotarbus jerami* gen. et sp. nov.

Diagnosis. Tiny trigonotarbid with a triangular carapace lacking an obvious median ridge.

Remarks. This diagnosis is not entirely satisfactory given the preservation of this specimen and the lack of obvious autapomorphies. *Eotarbus* is regarded as a plesion, representing the sister group of the triangular- and subtriangular-carapaced trigonotarbid families lacking lateral eye tubercles.

Eotarbus jerami gen. et sp. nov.

Text-figures 1–3

1990 Trigonotarbid; Jeram *et al.*, p. 658, fig. 1a–d.

Holotype and only specimen. Ulster Museum, Belfast, K 25850. Slide labelled as De.3.42/113.

Derivation of name. For Dr Andrew Jeram in recognition of his discovery of the specimen, and his work on fossil arachnids.

Diagnosis. As for the family.

Description. Holotype 1.35 mm long. Carapace 0.60 mm long with a basal width of 0.77 mm. Opisthosoma 0.75 mm long with a maximum width of 0.9 mm. Carapace triangular, lacking a strongly defined raised median region along the length of the carapace, but with a slight anterior projection. Posterior margin of carapace straight. Right hand margin of carapace better preserved than left. Probable median eyes present on slight raised tubercle 0.23 mm from the anterior tip of the carapace. Distinct pair of inverted 'V'-shaped grooves anterior to the eyes, either side of this raised area.

Coxosternal region partly complete with leg coxae 2–4 preserved and subtriangular in shape. Chelicerae, palpal coxae and leg coxae 1 absent. Coxae 2 and 3 arranged around a sternum, coxae 4 not distinct, but appear to attach to the body posterior to the sternum. Lengths of coxae in mm: 2, 0.25; 3, 0.31; 4, 0.36. Appendages generally not preserved. Trochanter of leg 2 present, 0.12 mm long, but apparently compressed. A single, fragmentary walking leg, probably leg 3 or 4, preserved, bent back beneath the ventral opisthosoma. Podomere lengths in mm as follows: femur (incomplete) 0.18; patella 0.18; tibia 0.20; basitarsus 0.15. Telotarsus not preserved.

Opisthosoma broadly oval. Division into median and lateral tergites present, but not distinct. Tergite 9 apparently lacking division into median and lateral plates. Approximate lengths of tergites along the midline in mm: macrotergite 2 + 3, 0.11; 4, 0.08; 5, 0.11; 6, 0.13; 7, 0.10; 8, 0.09; 9, 0.16. Posterior margins of anterior tergites straight, posterior margins of tergites 6–8 increasingly curved, though posterior margin of tergite 9 straighter. Posterior tergites 6–9 slightly displaced relative to the rest of opisthosoma with slight anticlockwise rotation. Ventral opisthosomal segmentation less distinct than dorsal. Segment 10 surrounding a pygidium present.

Remarks. *Eotarbus jerami* is the smallest trigonotarbid known, although it is impossible to determine whether or not it is a juvenile.

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A NEW OXYTOMID BIVALVE FROM THE UPPER JURASSIC–LOWER CRETACEOUS OF ANTARCTICA

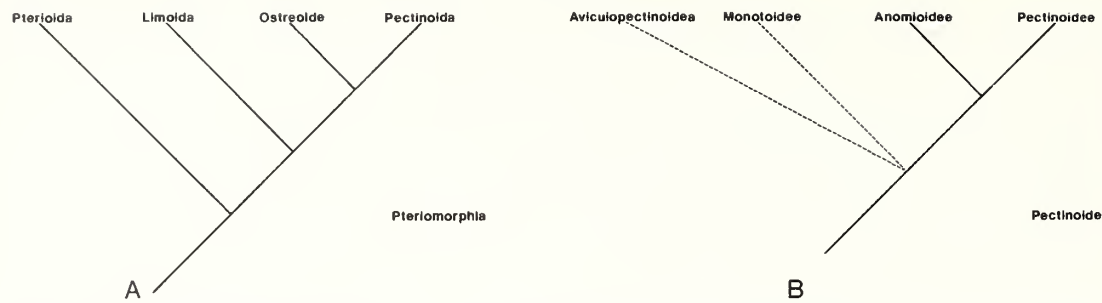
by J. A. CRAME

ABSTRACT. *Praeacellina umbonoradiata* gen. et sp. nov. is a small pteriomorph bivalve from the Upper Jurassic–Lower Cretaceous of Antarctica which can be referred to the family Oxytomidae, within the superfamily Monotoidea. Sub-rounded to strongly obliquely elongated in outline, it is markedly inequivalve. The left valve is somewhat narrower than the right, and the latter possesses a clearly defined, but tiny, antero-dorsal ear. This feature takes the form of a rounded blade which is strongly inclined with respect to the plane of commissure. This is a typical oxytomid feature, as is the presence of a pseudoctenolium. Indeed, there is now a considerable volume of morphological and stratigraphical evidence to suggest close phylogenetic ties with Late Jurassic–Early Cretaceous genera such as *Aucellina* and *Oxytoma*. Other austral oxytomids, such as *Arctotis* and *Maccoyella*, comprise a distinct morphological subgroup characterized by much thicker hinges. Whilst elucidation of the features of *Praeacellina* helps to consolidate the taxonomic differences between the Oxytomidae and Buchiidae, it highlights further possible similarities between the former of these categories and the Monotoidea. Resolution of phylogenetic relations within the Monotoidea will greatly assist studies of the evolution of Mesozoic high-latitude bivalve faunas.

WITHIN the class Bivalvia there are two major groupings of epifaunal bivalves with predominantly calcitic shells: the mussels (usually referred to the order Mytiloida within the subclass Isofilibranchia) and the scallops and their close relatives (referred to the subclass Pteriomorphia) (Carter 1980, 1990). The latter group was particularly common from the late Palaeozoic to the late Mesozoic, when forms such as the inoceramids, bakevelliids, pinnids, pectinids, limids and oysters were major components of marine benthic invertebrate assemblages. Indeed, such was their abundance that they have been used widely in stratigraphical, ecological and biogeographical studies; this is particularly so in mid- to high-latitude regions. Nevertheless, it is true to say that, despite their widespread utility in palaeontology, we still know comparatively little about the phylogenetic relationships of many pteriomorph groups.

From the pioneering observations made by Waller (1978), it is understood that there are four calcitic orders of pteriomorphs, with the pteriods being the most primitive (Text-fig. 1A) (N.B. the classification of pteriomorphs followed here is that of Carter (1990)). This is so because they possess a nacreo-prismatic shell; in all the other groups the inner aragonitic layers are some form of crossed-lamellar structure and in the outer calcitic layers prismatic structure has been largely or completely lost (Waller 1978; Carter 1990). Foliated calcite ultrastructure is a derived character state restricted to just the orders Ostreoida and Pectinoida (Text-fig. 1A). Within the order Pectinoida it has been suggested that four taxa of superfamily rank can be recognized: the essentially Palaeozoic Aviculopectinoidea, the essentially Mesozoic Monotoidea, and the Anomioidea and Pectinoidea, both of which comprise a variety of fossil and living forms (Table 1). The phylogenetic positions of the Aviculopectinoidea and Monotoidea are as yet unresolved, but it is assumed generally that both taxa were ancestral to the stock yielding the Anomioidea and Pectinoidea (Text-fig. 1B).

If the distinctive oyster-like anomioids are excluded, the order Pectinoida can be said to be characterized by small to large bivalves which are rounded to obliquely oval in outline, moderately to strongly inequivalve (LV always more inflated than RV), and typically bear stronger radial than concentric ornament. However, perhaps their most diagnostic feature is the presence of a small ear and byssal notch in the antero-dorsal region of the right valve. At some stage in their lives most



TEXT-FIG. 1. Schematic phylogenies for: A, the bivalve subclass Pteriomorphia, and B, the order Pectinoidea. Based on data contained within Waller (1978). In B the superfamily Aviculopectinoidea may well be the most primitive, as some representatives are known to possess a nacreous shell layer; such a feature is unknown within the Monotoidea (Carter 1990).

TABLE 1. Subdivision of the bivalve order Pectinoidea. Based on Hertlein *et al.* 1969 and Carter 1990, with minor amendments. Abbreviations: E, Early; L, Late; M, Mid.

Order PECTINOIDA Rafinesque, 1815	
Superfamily	Aviculopectinoidea Meek and Hayden, 1864
Family	Leiopectinidae Krasilova, 1959 (Ord.-E. Dev.)
	Pterinopectinidae Newell, 1938 (L. Sil.-E. Perm.; ?L. Perm.-E. Trias.)
	Aviculopectinidae Meek and Hayden, 1864 (L. Dev.-L. Trias.)
	Deltopectinidae Dickins, 1957 (L. Carb.-E. Perm.)
	Euchondriidae Newell, 1938 (L. Dev.-L. Perm.)
Superfamily	Monotoidea Fischer, 1887
Family	Monotidae Fischer, 1887 (L. Trias.-L. Jur.)
	Asoellidae Begg and Campbell, 1985 (L. Trias.)
	Buchiidae Cox, 1953 (?M. Perm.-E. Cret.)
	Oxytomidae Ichikawa, 1958 (E. Perm.-?E. Paleoc.)
	Pseudomonotidae Newell, 1938 (E. Carb.-E. Trias.)
Superfamily	Anomioidea Rafinesque, 1815
Family	Permanomiidae Carter, 1990 (Perm.)
	Anomiidae Rafinesque, 1815 (Jur.-Rec.)
	Placunicae Gray, 1840 (Eoc.-Rec.)
Superfamily	Pectinoidea Rafinesque, 1815
Family	Propeamussiidae Abbott, 1954 (E. Carb.-Rec.)
	Entoliidae von Teppner, 1922 (E. Carb.-L. Cret.)
	Pernopectinidae Nevesskaya <i>et al.</i> , 1971 (E. Carb.-L. Perm.)
	Streblochondriidae Newell, 1938 (E. Carb.-Perm.)
	Pectinidae Rafinesque, 1815 (Trias.-Rec.)
	Spondylidae Gray, 1826 (?E. Perm.-?L. Trias)

pectinoids have been anchored to the substratum by a byssus, and always with the flatter right valve underneath (i.e. pleurothetic on the RV). The largest and most obvious 'scallops', members of the Pectinoidea, are generally subequilateral, with the anterior ear and its posterior counterpart forming subequal wing-like extensions to the hingeline. A prominent triangular ligament pit directly beneath the umbones is commonly flanked by cardinal crura (or ridges), and a primitive prismatic calcite outer shell layer may be partially or wholly replaced by homogeneous or foliated calcite. Similarly, ancestral middle and inner layers of aragonitic crossed-lamellar structure may be replaced by foliated calcite (Waller 1978; Carter 1990).

Although both the anomioideans and pectinoideans form reasonably coherent groups, the same is not necessarily true of the aviculopectinoideans and monotoideans (Table 1). At least part of the

reason for this is that the aviculopectinoid family Aviculopectinidae shows considerable stratigraphical and morphological overlap with each of the five component families of the Monotoidea. Since its redefinition in the *Treatise on invertebrate paleontology* (Cox 1969), it is apparent that at least two genera should now be removed from the Aviculopectinidae: *Claraia* is probably better assigned to the Pterinopectinidae (Zhang 1980), and *Otapiria* to the Monotidae (Begg and Campbell 1985). Nevertheless, this still leaves Triassic taxa, such as *Leptochondria*, *Ornithopecten* and *Oxypteria*?, which bear very strong resemblances to the Monotoidea (Waller 1978, p. 363).

It has been assumed generally that the Monotoidea arose from the Aviculopectinoidea by the alteration of two basic features: loss of an inner aragonitic shell layer, and interruption of a once-continuous pallial line (Ichikawa 1958; Cox 1969). However, Carter (1990) has pointed out that the putative ancestral lineage within the Aviculopectinidae contains at least one taxon, *Linipecteu*, in which the outer prismatic calcite layer has been entirely replaced by homogeneous structure. As certain oxytomid genera, such as *Oxytoma* and *Meleagrinea*, still possess a thin outer prismatic calcite shell layer, and some species, such as *Meleagrinea curta* (Hall), may have a thin aragonitic middle shell layer in the right valve, an alternative ancestor may need to be found. *Pseudomonotis*, with its aragonitic middle and inner shell layers and at least some prismatic material in its outermost layer, is a possibility here, but it is apparent that its superfamilial placing is somewhat conjectural (Newell and Boyd 1970; Waller 1978; Carter 1990). Finally, it should be stressed that the familial subdivision of the Monotoidea has been the subject of considerable debate (see extended discussion in Ichikawa 1958; Begg and Campbell 1985; Crame 1985; Carter 1990).

It is important to emphasize that resolution of these taxonomic problems may have considerable palaeobiogeographical implications. For example, within the superfamily Monotoidea a surprising variety of taxa displays either widespread or cosmopolitan distributions, and elucidation of their phylogenetic relationships should provide important insights into the origin and evolution of high-latitude marine biotas. Of the seven Mesozoic genera currently assigned to the family Oxytomidae (*sensu* Crame 1985), two are essentially cosmopolitan (*Oxytonia* and *Meleagrinea*), two are bipolar (*Arctotis* and *Aucellina*), and three are associated with just the southern high-latitude regions (*Malayonaorica*, *Maccoyella* and *Pseudavicula*) (Cox 1940; Kobayashi and Ichikawa 1952; Ichikawa 1958; Begg and Campbell 1985; Crame 1985, 1986). As a prelude to a full phylogenetic revision of the Monotoidea, its component genera are being reassessed in terms of morphological features (especially those of the hinge-line and shell structure) which may form potential synapomorphic character suites. Particular attention has been paid so far to the Oxytomidae, and during the course of recent fieldwork in Antarctica a new form was found which is stratigraphically intermediate between Late Jurassic (i.e. Kimmeridgian–Tithonian) taxa such as *Oxytoma* and *Arctotis* and the Early Cretaceous (?Late Barremian–Albian) *Aucellina* (Crame and Howlett 1988; Crame *et al.* 1993). It is the intention of this study to describe this new form and assess its phylogenetic and biogeographical potential.

All the specimens described in this study are deposited in the collections of the British Antarctic Survey, Cambridge, UK.

SYSTEMATIC PALAEONTOLOGY

Class BIVALVIA Linnaeus, 1758

Subclass PTERIOMORPHIA Beurlen, 1944

Order PECTINOIDA Rafinesque, 1815

[*emend.* Waller 1978, p. 353; Carter 1990, p. 234]

Superfamily MONOTOIDEA Fischer, 1887

[*nom. transl.* Begg and Campbell 1985; *emend.* Carter 1990]

Diagnosis. See Waller 1978, p. 362; Begg and Campbell 1985, p. 727; Carter 1990, p. 245.

Family OXYTOMIDAE Ichikawa, 1958

Emended diagnosis. Extended diagnoses and discussions have been given by Ichikawa (1958, p. 158), Begg and Campbell (1985, p. 735), Crame (1985, p. 36) and Carter (1990, p. 249). The salient features which serve to distinguish oxytomids are as follows: LV-profile can be more upright and subsymmetrical; low, rounded antero-dorsal wing commonly developed; hinge edentulous but anterior portion may bear accessory tooth-like features which articulate with inner surface of RV ear; anterior portion of hinge-line may bear shallow sulcus but this is in no way equivalent to the *Gelenkgrube* of the Buchiidae; radial ornament predominates over concentric. RV has a more rounded profile; antero-dorsal ear comparatively long and blade-like; ear not folded or turned strongly inwards; anterior portion of ligament area continues along dorsal surface of ear almost to its tip; ear tilted strongly inwards (with respect to the plane of commissure) and rests snugly beneath antero-dorsal region of LV; byssal notch can be comparatively broad; pseudoctenolium may be present; ornament typically more subdued than on LV; thin outer shell layer of prismatic calcite; thin middle shell layer of aragonitic crossed-lamellar structure may also be present.

Component genera. *Oxytoma* Meek (*sensu lato*) (?Olenekian–Danian), *Meleagrinnella* Whitfield (Rhaetian–Tithonian), *Arctotis* Bodylevsky (Lias–Hauterivian), *Maccoyella* Etheridge, Jr (Aptian–Albian), *Pseudavicula* Hudleston (Aptian–Albian), *Avicularca* von Bubnoff? (Carnian–?Rhaetian). A Permian member of the family, *Cyrtostro* Branson (Cox 1969), has not been considered in this study.

Remarks. Reference is again made to the previously cited sources for a full discussion of the taxonomic status of the Oxytomidae. In summary, it can be stated here that the boundaries between at least four of the component families of the Monotoidea (Monotidae, Asoellidae, Buchiidae and Oxytomidae; Table 1) are by no means rigid. The Buchiidae can usually be distinguished from the Oxytomidae by features such as a smoother form, largely opisthodontic ligament, and thickened, spoon-shaped anterior ear on the RV (Crame 1985). Articulation of the tip of this ear with a deeply recessed pit (*Gelenkgrube*) on the anterior of the LV hinge may prove to be a synapomorphy for the Buchiidae, but this feature needs further investigation. Shallower articulation pits (again, sometimes referred to as *Gelenkgrube*) have been recorded along the LV hinges of certain oxytomids (e.g. *Meleagrinnella*; Cox 1940, p. 91). Monotids can usually be distinguished by their much stronger radial ornament and tiny RV ear. Nevertheless, there are indications that the hinge region of this group, although somewhat smaller, is not significantly different in form from that of the Oxytomidae (e.g. Payevskaya 1985; Grant-Mackie and Silberling 1990). The simple hinge and large, blade-like ear may serve to establish the genera *Asoella* and *Etalia* within the family Asoellidae (Begg and Campbell 1985), but the assignment of *Aucellina* here is questionable. Some forms of *Aucellina* exhibit a prominent pseudoctenolium (e.g. Woods 1905, pl. 10, fig. 9b), and this feature almost certainly links it closely with *Oxytoma*.

Genus PRAEAUCELLINA gen. nov.

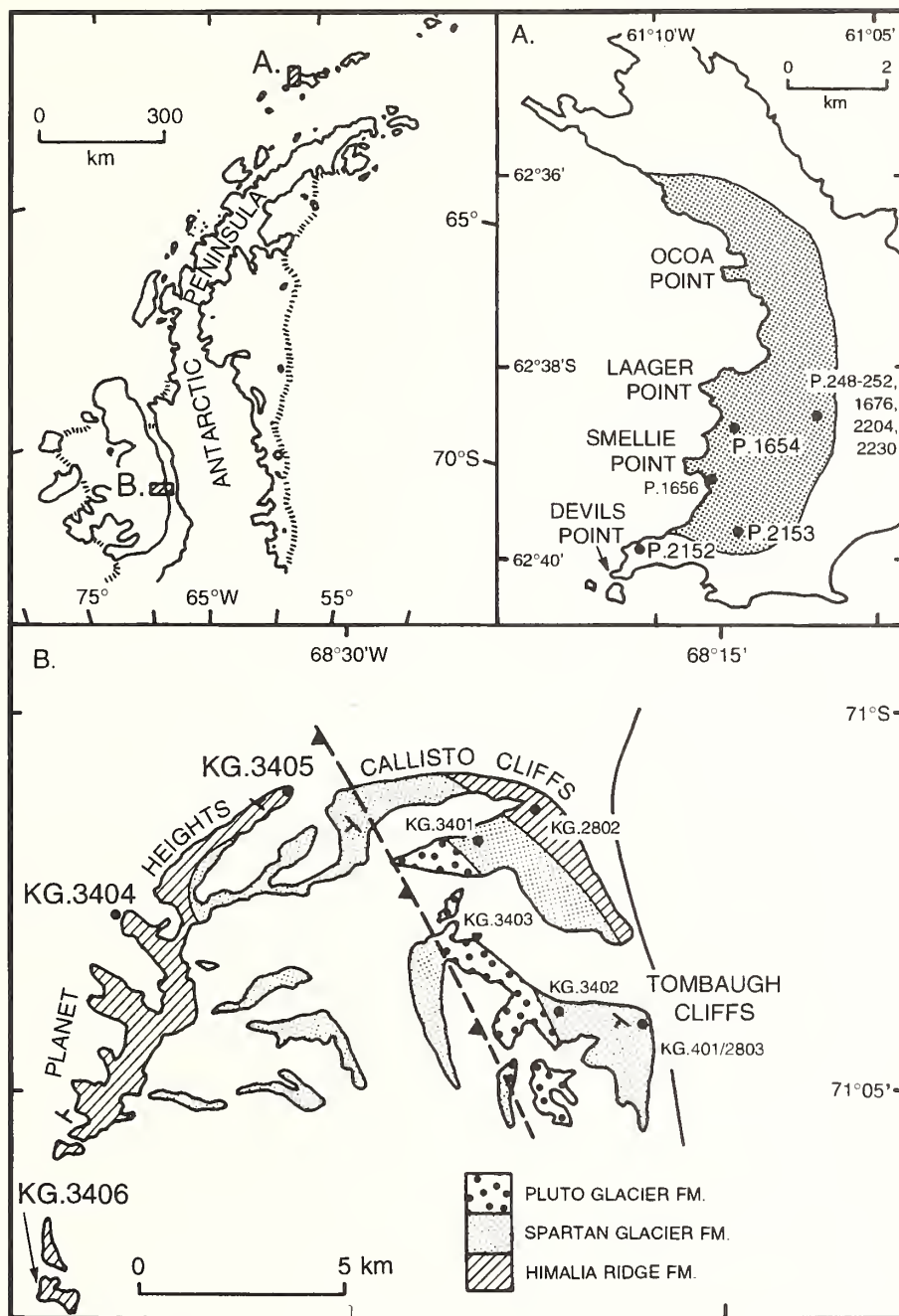
Derivation of name. Latin: *prae* (in front of: a forerunner), referring to the fact that this taxon may well be an ancestor of the well known oxytomid genus, *Aucellina*. Gender feminine.

Type species. *Praeaucellina umbonoradiata* gen. et sp. nov.

Other species. The genus is monotypic.

Diagnosis and remarks. As for the type species, see below.

Occurrence. Lower Cretaceous (Berriasian) of the Byers Group, western Livingston Island, and Upper Jurassic (Tithonian)–Lower Cretaceous (Berriasian) of the Fossil Bluff Group, Alexander Island; both these localities lie off the west coast of the Antarctic Peninsula. Further details given below.



TEXT-FIG. 2. Locality map for the Antarctic Peninsula region. Inset A shows the western margins of Byers Peninsula, Livingston Island, South Shetland Islands. Shaded area represents the outcrop of the President Beaches Formation; more extensive geological map given in Crame *et al.* (1993). Inset B shows localities within the Fossil Bluff Group of eastern Alexander Island. The Jurassic-Cretaceous boundary is located within the Himalia Ridge Formation (see also Crame and Howlett 1988, fig. 1).

Praeaucellina umbonoradiata gen. et sp. nov.

Text-figures 4A–S, 5A–B, 6A–B

- vp 1984 *Otapiria* sp. nov. 1; Crame, pl. 2, fig. 6 (*non* pl. 2, fig. 5).
 v. 1984 *Otapiria* sp. nov. 2; Crame, pl. 2, figs 3–4.
 v. 1984 *Buchia* sp. nov. (small form); Crame and Howlett, fig. 10b–c.

Derivation of name. Latin: *umbo*; *radiata* (radiate, bearing rays); referring to the common restriction of fine, radial ornament to the umbonal regions of the shell.

Type material. Holotype: P.250.36 (Text-fig. 4A; internal mould LV). Paratypes: P.248.9; P.250.3b, 4, 6a–c, 8, 10, 11a–d, 14, 17a, b, 31–32, 34, 38–41, 44–45, 55, 64, 176; P.251.2a–c; P.252.3, 5; P.1654.33, 36, 45; P.1656.14, 24, 30–31, 39, 47, 51, 53, 70, 72, 75–78, 80, 82–84, 86–87; P.1676.1a–b, 2–4, 7–9, 14–16, 25; P.2152.20; P.2153.11, 21–23, 26–27, 31–32, 34, 37, 53–54, 56, 57b, 61, 90–129; P.2204.7, 9–10, 11a–c, 13, 15; P.2230.7, 9, 21, 23; KG.2802.346–348, 501–503, 516, 518–519, 530, 547, 553, 560, 570, 610; KG.2803.6, 31, 37, 47, 59, 65; KG.3404.302–306, 308–311, 313, 388, 415, 418a–b, 450; KG.3405.8.

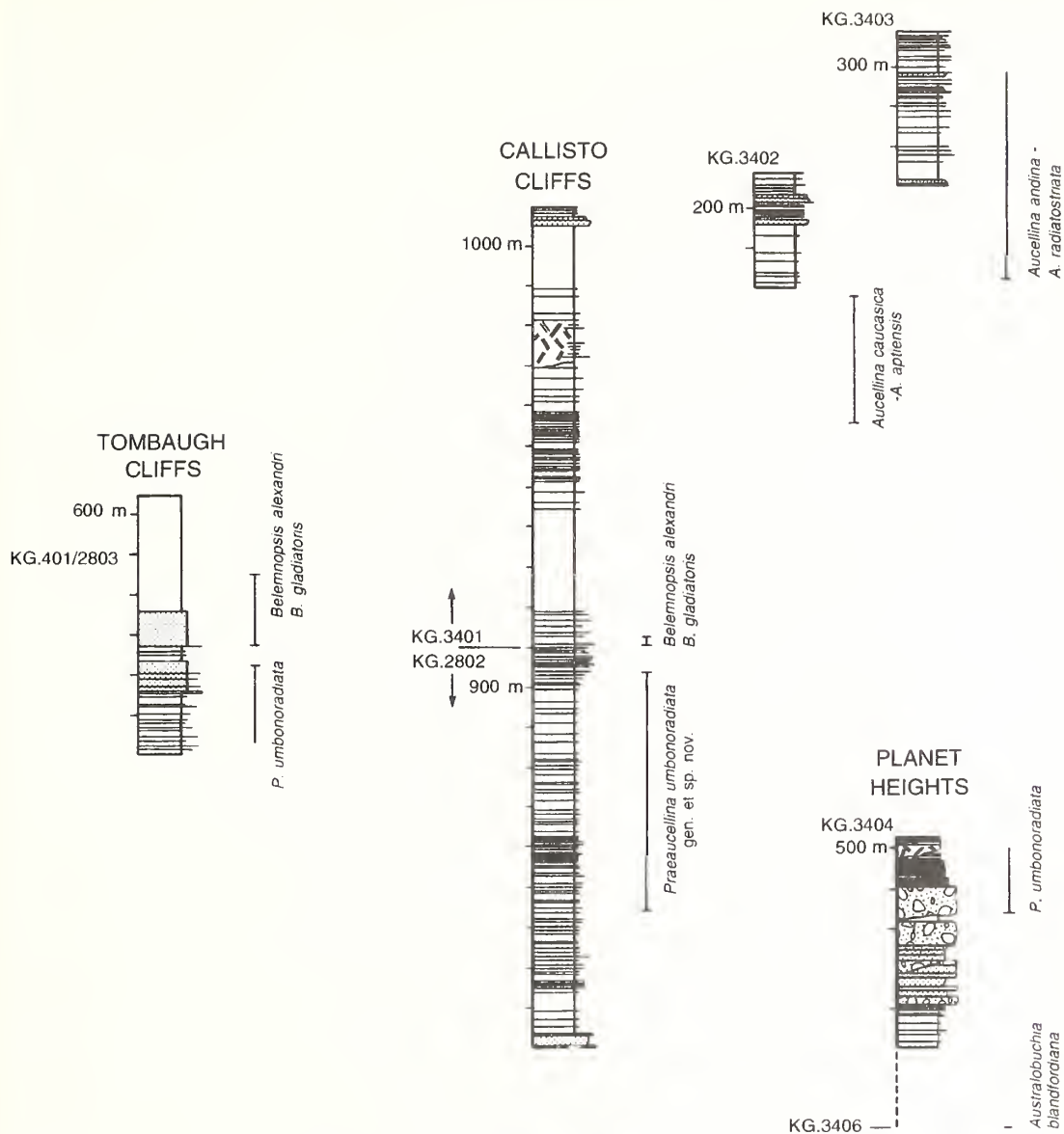
Most of the specimens prefixed by 'P.' are from the President Beaches Formation, Byers Group, western Livingston Island; however, those from locality P.2152 are from the overlying Chester Cone Formation (Text-fig. 2). Whereas the former of these stratigraphical units is Berriasian, the latter is probably Berriasian–Valanginian (Crame *et al.* 1993). *Praeaucellina umbonoradiata* gen. et sp. nov. occurs in mudstone-dominated lithologies in association with a bochianitid-spiticeratid ammonite assemblage and bivalves such as the pergamiid *Manticula*, a small *Inoceramus*, nuculids, grammatodontids and several small heterodonts. Dense bedding plane assemblages in the lower levels of section P.2153 were nucleated on the shafts of bochianitid ammonites; only a small, representative sample of these specimens has been included in this study.

Specimens prefixed by 'KG.' are from the uppermost levels of the Himalia Ridge Formation, Fossil Bluff Group, eastern Alexander Island (Text-fig. 2). These levels are of undifferentiated Upper Tithonian–Upper Berriasian age (Crame and Howlett 1988). At locality KG.2802 the specimens occur between approximately 338–925 m in the measured section; at KG.2803 they occur within the lower 200 m of the section, and at KG.3404 between 438–528 m. KG.3405 is an isolated spot locality (Text-figs 2–3) (Crame and Howlett 1988). In Alexander Island, *Praeaucellina umbonoradiata* gen. et sp. nov. occurs in association with a berriasellid ammonite-belemnopseid belemnite assemblage. Prominent co-occurring bivalves include *Retroceramus everesti* (Oppel), *Grammatodon*, *Pinna*, *Entolium* and other taxa suggestive of a mid- to outer-shelf setting.

Diagnosis. Small-medium oxytomid; LV varies in outline from rounded-quadrate to strongly obliquely elongate; LV typically only weakly inflated and non-gryphaeoid; RV subrounded to obliquely elongate; tiny RV ear is blade-like and tilted strongly inwards towards LV; deep, curving byssal notch and pseudoctenolium; essentially alivincular ligament; generally subdued concentric ornament, but fine, sharp radial ribs which are concentrated over the umbonal region.

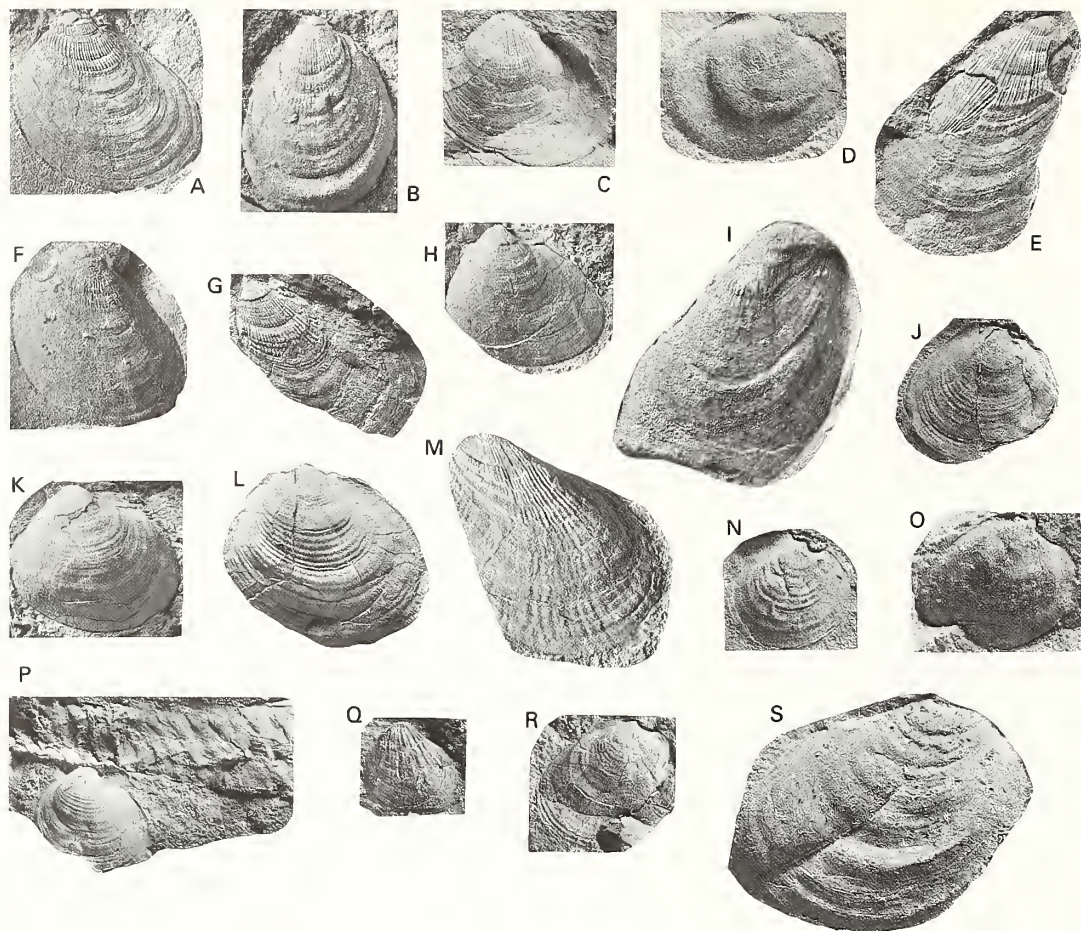
Description. Small-medium sized (for an oxytomid). Mean shell length (L , the distance from the beak to the maximum extremity of the ventral margin) of LVs is 11.9 mm (S.D. = 5.7 mm, $N = 95$), and for rights is 11.8 mm (S.D. = 5.2 mm, $N = 95$). The inequivalve nature of the shell is reflected in the somewhat narrower LV (as defined by the width, W , the maximum dimension perpendicular to L ; $\bar{x} = 9.3$ mm, S.D. = 4.2 mm, $N = 95$) compared with RV ($\bar{x}W = 10.8$ mm, S.D. = 4.2 mm, $N = 95$). These respective widths are significantly different (Student's t -test, $0.01 < P < 0.05$), as are the respective W/L ratios ($\bar{x}W/L$ LV = 0.74, S.D. = 0.2 mm, $N = 95$; $\bar{x}W/L$ RV = 0.9, S.D. = 0.2 mm, $N = 95$) ($P < 0.001$). All specimens preserved as internal or external moulds; however, some bear fragments of original shell material.

The largest LVs are typically moderately to strongly obliquely elongate. From a prominent, pointed beak, which rises above the hingeline and ranges from orthogyrous to slightly opisthogyrous, there is a straight to gently convex antero-dorsal margin which passes into well-rounded antero-ventral and ventral margins. The postero-dorsal margin is typically straight to gently rounded and may delineate a narrow wing (e.g. Text-fig. 4H, L). Smaller (i.e. juvenile) left valves often have a more rounded-quadrate profile; indeed, in some of these there is even a tendency to develop a small antero-dorsal wing. These small specimens are typically more strongly and evenly inflated than the larger ones (e.g. Text-fig. 4K–L). Left valve ornament comprises a combination of very fine radial ribs and low concentric folds. The radial ribs are so fine on many specimens (< 0.3 mm) as to qualify for description as striae; this is particularly so in the earliest stages of some specimens



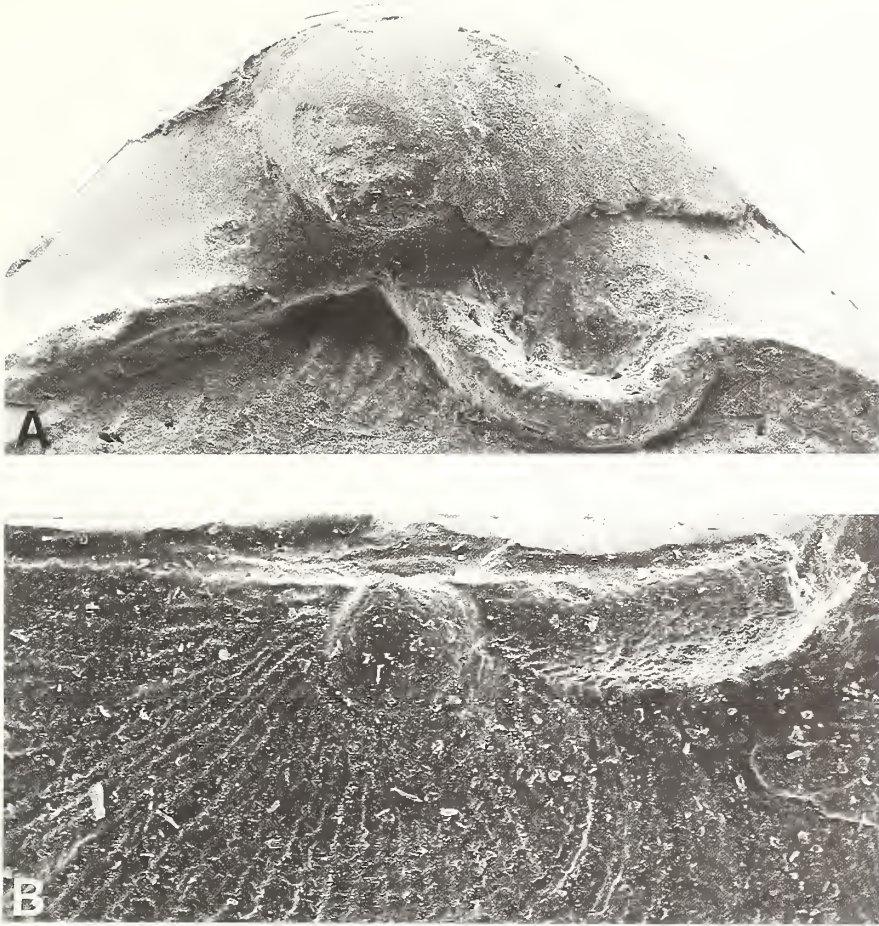
TEXT-FIG. 3. Stratigraphical correlations within the Fossil Bluff Group of eastern Alexander Island. *Praeacellina umbonoradiata* gen. et sp. nov. occurs consistently beneath the earliest representatives of *Aucellina*. The boundary between the Himalia Ridge and Spartan Glacier formations occurs at the junction between sections KG.2802 and KG.3401 at Callisto Cliffs; that between the Spartan Glacier and Pluto Glacier formations occurs at 1050 m in section KG.3401 (Callisto Cliffs) (see also Crame and Howlett 1988, fig. 9).

where very narrow secondaries occur intercalated between more prominent primaries (e.g. Text-fig. 4A–C). Superficially, the radial ribs appear to be more or less straight, but closer inspection reveals regular displacement where they cross concentric folds or depressions. They are confined essentially to the umbonal region of the valve (e.g. Text-fig. 4A–C, F–G). Concentric ornament comprises very fine growth lines which are only occasionally developed into moderately strong, regular rugae (e.g. Text-fig. 4L). In addition, broader concentric furrows, linked to distinct growth pauses, are variably developed.



TEXT-FIG. 4. *Praeacuellina umbonoradiata* gen. et sp. nov.; Tithonian–Berriasian of the Antarctic Peninsula region. A, holotype P.250.36; internal mould. B, paratype P.250.17a; internal mould LV. C, paratype P.251.2; rubber peel from an external mould LV. D, paratype P.250.45; internal mould RV. E, paratype P.250.4; incomplete internal mould RV. F, paratype P.250.31; rubber peel from external mould LV. G, paratype P.1676.1; internal mould LV. H, paratype P.2153.95; internal mould LV. I, paratype P.2204.13; rubber peel from an external mould RV. J, paratype P.1656.83; internal mould RV. K, paratype P.2153.101; internal mould LV. L, paratype P.2153.61; internal mould LV. M, paratype P.2204.7; internal mould LV. N, paratype P.1656.72; internal mould RV. O, paratype KG.3404.311; internal mould RV. P, paratype P.2153.132; internal mould LV attached to the shaft of a *Bochiante* ammonite. Q, paratype P.1656.30; internal mould of a juvenile LV. R, paratype P.2153.122; internal mould RV. S, paratype, rubber peel from an incomplete external mould RV (P.250.8). All specimens from the Berriasian President Beaches Formation, Byers Group, western Livingston Island, except O which is from the Tithonian–Berriasian Himalia Ridge Formation, Fossil Bluff Group, eastern Alexander Island. All specimens $\times 1.5$, except O which is $\times 3$.

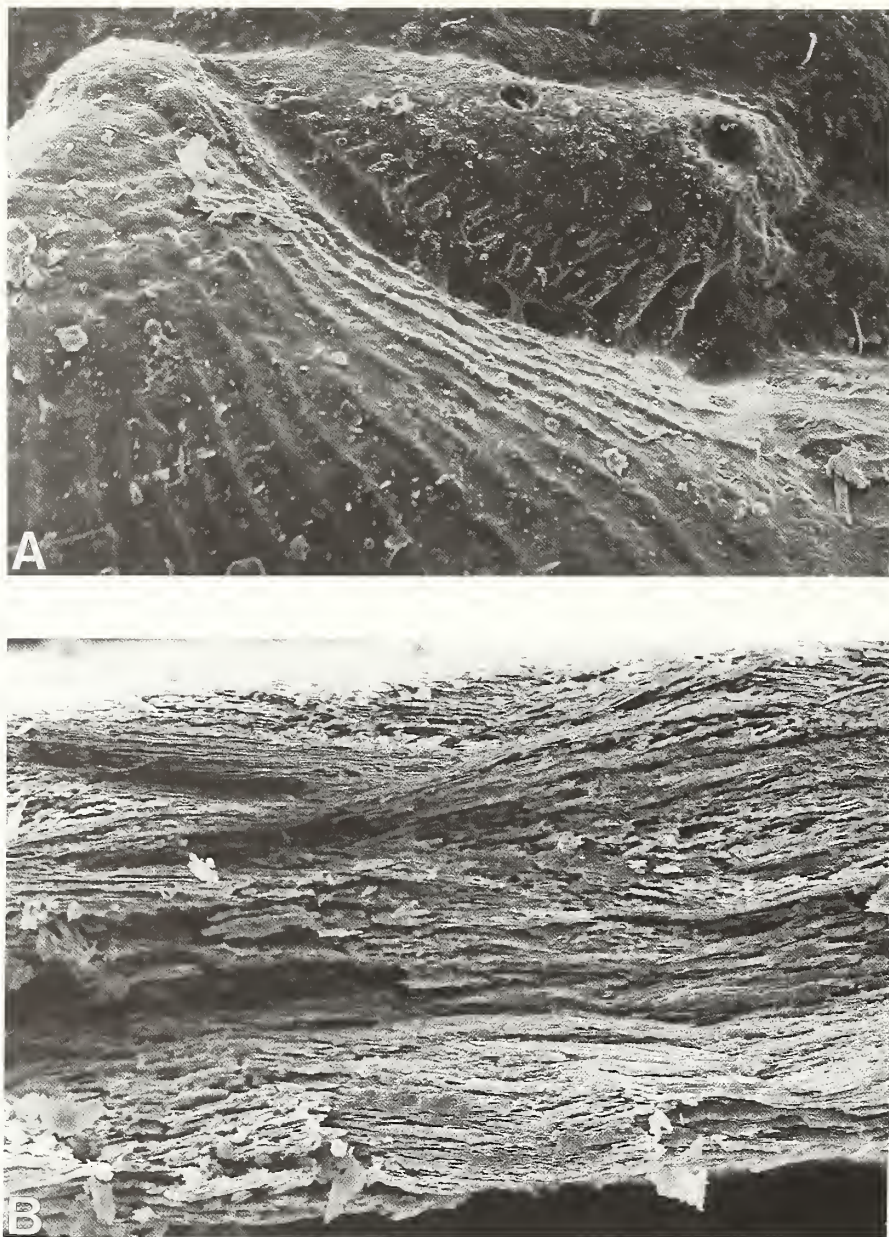
Right valve outlines vary from strongly obliquely elongate (e.g. Text-fig. 4E, I) to those which are considerably more rounded (e.g. Text-fig. 4J, N–O). In the latter forms the anterior margin is noticeably shorter and more convex, and there is a narrowly demarcated postero-dorsal wing. Right valves are typically slightly less inflated than left valves and many bear only traces of faint concentric ornament. However, the distinctive radial ornament is present on a number of both small and large specimens; it is again restricted largely to the umbonal region (Text-fig. 4E, I). The most distinctive feature of the right valve is a tiny antero-dorsal ear.



TEXT-FIG. 5. The hinge region of *Praeaucellina umbonoradiata* gen. et sp. nov. A, P.2153.133; left valve hinge region viewed from the inside and slightly from above. The posterior portion of the hinge (to the left) is relatively straight, but the anterior takes the form of shallow, sinusoidal curve. Initially, the anterior portion resembles a protruding lobe, with a concave depression on its upper surface; it then passes into a curving, recessed area. SEM, $\times 30$. B, P.2153.134; right valve hinge region, viewed from the outside and slightly from above. In a fully articulated specimen, the anterior ear (to the right) fits against and beneath the prominent bulge in the anterior region of the LV hinge. The apex of a broad, triangular resiliifer is located just beneath the top of the cap-like prodissoconch. SEM, $\times 65$.

Commonly no more than about 1.5 mm long, this feature takes the form of a gently curving blade which is tilted strongly inwards so that its upper surface comes to lie against, and largely underneath, the anterior region of the left valve hinge (Text-figs 4N, 5). The latter typically has a sinusoidal form, bulging out initially at its point of contact with the right valve ear and then curving inwards. The upper surface of the sinusoidal bulge may take the form of a shallow depression (Text-fig. 5A). As far as can be detected, the hinge and ligament surface of the left valve are essentially smooth; no form of tooth or socket has been detected.

In the right valve it is apparent that the ligament area extends along the dorsal surface of the ear, almost to its extremity. In its centre there are traces of a distinct, obtuse-angled triangular pit (or resiliifer), the apex of which lies directly beneath the beak (as marked by a smooth, cap-like prodissoconch of some 250 μm diameter) (Text-fig. 5B). The sides of the pit diverge away from the beak at an angle in excess of 130° and its



TEXT-FIG. 6. *Praeacuellina umbonoradiata* gen. et sp. nov. A, P.2153.135; enlargement of the RV anterior ear to show pseudoctenolium. The latex peel from an external mould shows a broad, blade-like ear expanding from the beak region. The row of teeth-like ridges and sockets forming the pseudoctenolium is located along the ventral margin of the ear; they abut a deep, channel-like byssal notch which curves in sinusoidal fashion from the beak to the free tip of the ear. SEM, $\times 100$. B, P.2153.136; fragment of original shell material from the central region of a LV. Section normal to the shell surface (uppermost) to show crossed-foliated shell structure. SEM, $\times 1000$.

base may be slightly curved. The right valve ligament would thus appear to conform to the classic alivincular form; further details of the left valve ligament are not yet known. The right anterior ear is clearly separated from the main disc of the shell by a narrow and deep byssal notch. This can be traced from the anterior tip (where it is at its widest) to the prodissoconch, and on its upper border (i.e. the ventral surface of the ear) there is a distinct comb-like row of teeth (Text-fig. 6A). These constitute a pseudoctenolium (*sensu* Waller 1984).

Original shell material is preserved on a number of small specimens, especially from locality P.2153 (Text-fig. 2A). Unfortunately, this is nearly all in a poor state of preservation and it has not yet been possible to examine variation in shell structure on a systematic basis. The dominant material, on both left and right valves, is a form of crossed-foliated calcite in which rather poorly defined first order lamellae intersect at a comparatively low angle (Text-fig. 6B). No trace of a prismatic calcite layer or any form of aragonite has yet been found in either valve.

Remarks. The general form of this bivalve links it firmly with the superfamily Monotoidea, and the spatulate, strongly inclined right valve ear suggests particular affinity with the Oxytomidae. Such a connection is strengthened by the presence of a pseudoctenolium, which is also present in both *Oxytoma* Meek (?Olenekian–Danian) and *Aucellina* Pompeckj (Barremian–Cenomanian) (Cox 1940; Duff 1978; Waller 1978, 1984). *Praeaucellina* is particularly similar to the latter form, but may be distinguished consistently by the following criteria: its smaller size (*Aucellina* typically having a shell length in the 20–30 mm range); the less strongly inflated and less gryphaeoid form of the left valve; restriction of radial ornament to essentially the umbonal region of both valves (for comparative *Aucellina* specimens see Cox 1953, pl. 1, figs 1–10 and Macellari 1979, pls 1–2). Nevertheless, it should be stressed that, in form alone, right valves of the two genera are very similar. There are some valves too (e.g. P.2204.7; Text-fig. 4M), in which radial ornament does indeed stretch across the entire width of the valve; such forms are very difficult to separate from small *Aucellina*.

The presence of dense radial ornament on a number of specimens also raises the question of allegiance with another monotoidean family, the Monotidae Fischer (?Carnian–Tithonian; Table 1). Although generally held to be readily distinguishable by their thinner-shelled and less inflated form, stronger radial ornament and tiny right valve ear, it is apparent that representatives of this taxon do show considerable morphological overlap with the Oxytomidae; this is particularly so for the finely ribbed members of the genus *Otapiria* Marwick. Indeed it is not easy, at first sight, to separate certain Jurassic species of *Otapiria*, such as *O. marshalli* (Trechmann 1923, pl. 15, figs 6–9) and *O. tailleuri* Imlay (1967, pl. 1, figs 1–23) from some Cretaceous *Aucellina* (see e.g. Cox 1953, pl. 1, figs 1–9). *Otapiria* can be distinguished from *Praeaucellina* by its shape, more variable valve outlines (especially LV), and stronger radial ornament; nevertheless, the differences here are by no means profound.

Recent observations on the hinge region of both *Monotis* (*sensu lato*) and *Otapiria* have revealed the presence of a subcentral, triangular resilifer, and a tiny, blade-like ear in the right valve which is strongly inclined towards the left (Ando 1987, 1988; Grant-Mackie and Silberling 1990). Furthermore, it is apparent that both genera are characterized by a pseudoctenolium (e.g. Marwick 1935, pl. 34, fig. 4; Ando 1988, fig. 4). There would appear to be very close phylogenetic ties between the Monotidae and Oxytomidae (see below).

SOME STRATIGRAPHICAL AND PHYLOGENETIC CONSIDERATIONS

Associated macro- and microfossils confidently establish the age of *Praeaucellina umbonoradiata* gen. et sp. nov. in the President Beaches Formation, Byers Peninsula as Berriasian (Crame *et al.* 1993). Furthermore, all known occurrences of this species lie beneath the Valanginian ammonite-belemnite assemblage obtained from the Sealer Hill Member (Crame *et al.* 1993). The less well preserved specimens of *P. umbonoradiata* gen. et sp. nov. from Alexander Island are all located within the Upper Tithonian–Lower Berriasian upper levels of the Himalia Ridge Formation (Crame and Howlett 1988; Text-figs 2–3); again, all localities are below a distinctive Valanginian ammonite-belemnite assemblage in the base of the Spartan Glacier Formation (Text-figs 2 and 3).

The first occurrences of the genus *Aucellina* are within the higher levels of the Spartan Glacier Formation (Text-fig. 3). Initially, these are finely ribbed forms that are referred provisionally to an *A. caucasica* (Abich)–*A. aptiensis* d'Orbigny species group (?Barremian in age); these in turn lie stratigraphically below the more familiar southern forms, *A. andina* and *A. radiatostriata* (Aptian–Albian; Cox 1953; Crame and Howlett 1988). The long stratigraphical sections of eastern Alexander Island confirm that *Praeaucellina* is the older taxon and in phylogenetic terms it is the very probable ancestor of *Aucellina*.

The possible ancestral relations of *Praeaucellina* are less clear. Within the Jurassic Oxytomidae, *Oxytoma* is the most realistic putative ancestor as it has a closely comparable hinge region and right valve anterior ear. *Arctotis*, in comparison, has a somewhat broader and thicker hinge, and a different style of ornament; it would seem to be more closely related to the Aptian–Albian genus, *Maccoyella* (Crame 1985). An alternative link between *Praeaucellina* and the Monotidae could be established through the occurrence of taxa such as *Otapiria masoni* Marwick (1953, pl. 11, figs 10–11) in the Ohauan (Tithonian) of New Zealand. However this sole Late Jurassic representative of the Monotidae is still poorly known and its precise taxonomic status needs to be confirmed. In the Himalia Ridge Formation of eastern Alexander Island (Text-fig. 2), *Praeaucellina umbonoradiata* gen. et sp. nov. may occur only a few hundred metres above the last records of *Australobuchia blanfordiana* (Stoliczka) (Text-fig. 3). Unfortunately, the hinge region of this form too, is still imperfectly known and it is not yet possible to distinguish clearly between the southern buchiids and oxytomids.

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CHITINOZOA OF THE SILURIAN–DEVONIAN BOUNDARY SECTIONS IN PODOLIA, UKRAINE

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ABSTRACT. The Upper Silurian and Lower Devonian beds along the Dnestr River and its tributaries form one of the sections discussed as a possible international Global Stratigraphic Stratotype and Point (GSSP) for the Silurian–Devonian boundary. On the basis of the co-occurrence of a graptolite (*Monograptus uniformis angustidens*) and a conodont (*Ieriodus woschmidti*) this boundary was drawn at the base of the Tajna Formation. However, chitinozoans from these strata are typical of Přídolí chitinozoan assemblages, and include the index species, *Urnochitina urna*, and other taxa, e.g. *Calpichitina annulata*, *Linochitina klonkensis*, in the lower part of the Tajna Formation. Early Lochkovian chitinozoans, especially the index species *Eisenackitina bohemica* and associated taxa, e.g. *Margachitina catenaria*, *Pterochitina megavelata*, *Calpichitina velata*, *Cingulochitina ervensis*, are present in the upper part of the Tajna Formation. The Silurian–Devonian boundary should therefore be drawn in the middle part of the Tajna formation. Neither late Lochkovian nor early Pragian chitinozoan species have been recorded in the investigated material. The differences noted in the respective ranges of the chitinozoan and graptolite index species in Podolia and Bohemia, suggest that the section containing the stratotype for the base of the Devonian in Bohemia may be less complete than the sequence exposed in Podolia. The Přídolí and Lochkovian chitinozoan assemblages from Podolia show striking similarities to those from south-east Poland, Bohemia and from some northern Gondwana localities. A new species, *Angochitina tsegelnjuki* sp. nov., is described.

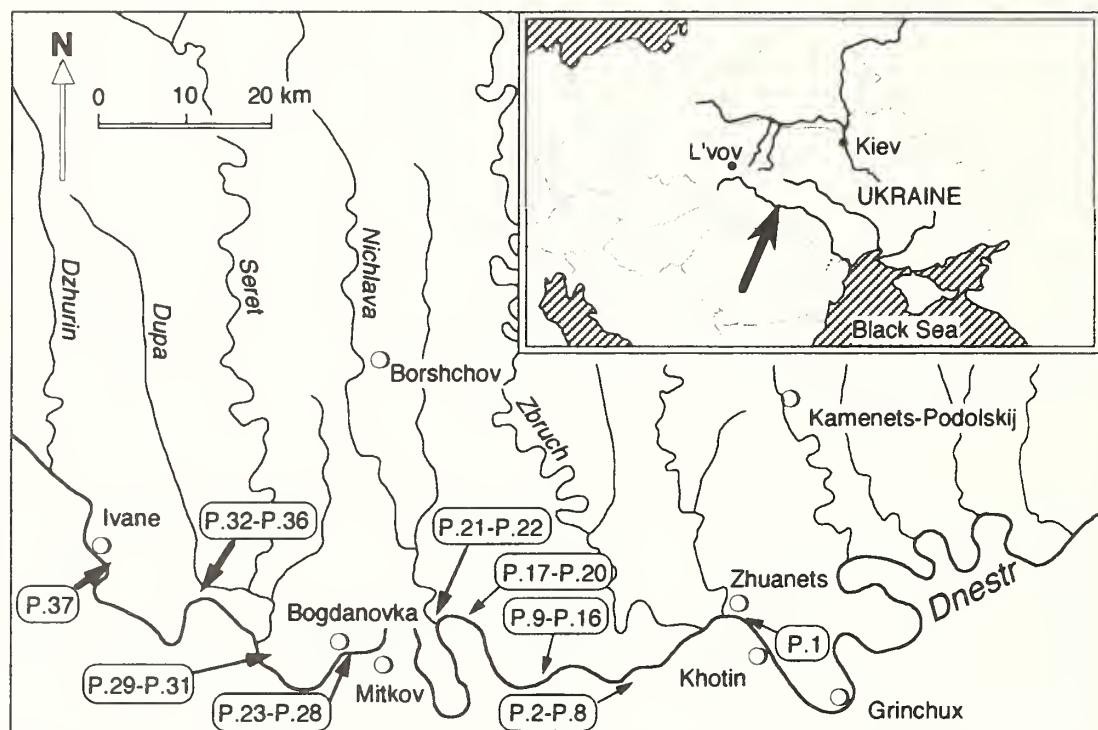
PIONEERING work on the Lower Palaeozoic of Podolia during the nineteenth century attracted the attention of many palaeontologists and stratigraphers. The first biostratigraphical investigation was carried out by Kozłowski (1929), who worked on upper Silurian and lower Devonian brachiopod faunas. The Silurian was further subdivided by Nikiforova in a series of papers (e.g. Nikiforova 1948, 1954). More recent contributions are those of Nikiforova and Predtechenskij (1968), Tsegelnjuk *et al.* (1983) and Koren' *et al.* (1989). The Upper Silurian and Lower Devonian exposures along the Dnestr River were investigated in detail (Nikiforova and Predtechenskij 1968; Nikiforova 1977) as a possible international stratotype for the Silurian–Devonian boundary. The uppermost Silurian (Skala 'horizon') was also one of the candidates for the fourth series of the Silurian (Tsegelnjuk *et al.* 1983; Abushik *et al.* 1985). Information about chitinozoan faunas from Podolia is available from four papers. The Ordovician (Ashgill) and early Silurian faunas were briefly discussed by Laufeld (1971); Obut (1973) illustrated chitinozoans from Silurian and Lower Devonian beds; and Silurian chitinozoans were described or listed by Tsegelnjuk (1982) and Tsegelnjuk *et al.* (1983). Other palynomorphs, including Silurian acritarchs (Kirjanov 1978) and a few early Devonian miospores (Arkhangelskaya 1980) have also been reported from the Dnestr River area.

Podolia was a part of Baltica during the Early Palaeozoic (e.g. see Paris and Robardet 1990) and the same chitinozoan faunas could therefore be expected to be present in Podolia and Baltoscandia. This is obvious from Laufeld's paper, but the precise provenance of the chitinozoan faunas described by Obut and Tsegelnjuk is not clear. We therefore found it necessary to review the Late Silurian and Early Devonian chitinozoans from Podolia, and to compare them with contemporary faunas from nearby south-east Poland (Wrona 1980), and to the faunas of the Upper Silurian and Lower Devonian boundary stratotypes in Bohemia (Paris 1981; Paris *et al.* 1981; Paris and Kříž 1984; Chlupáč *et al.* 1985; Kříž *et al.* 1986).

The samples were collected by Sven Laufeld during the Third International Symposium on the Silurian–Devonian boundary excursion to Podolia in 1968.

BRIEF OUTLINE OF THE UPPER SILURIAN-LOWER DEVONIAN STRATIGRAPHY OF PODOLIA

The Dnestr Basin of Podolia was occupied by a shallow epicontinental sea that existed in the south-western part of the Russian Platform during most of the Silurian and early Devonian. Lower Cambrian to Lower Devonian beds crop out along the Dnestr River and its northern tributaries from Molodovo to Ustechko villages, a distance of about 100 km (Text-fig. 1). In general the dip



TEXT-FIG. 1. Schematic location map of the sampled localities along the Dnestr River, Podolia, Ukraine. Adapted from Nikiforova and Predtechenskij (1968) and Koren' *et al.* (1989).

is $1-2^{\circ}$ towards the west-south-west, but it may locally reach $5-6^{\circ}$. The stratigraphical division of the Silurian and Devonian is based on lithology and to some extent on facies reconstructions. The lithologies and the fossil content of the different formations and members have been described in several papers (for references see above). The descriptions below are based mainly on the results published by Nikiforova and Predtechenskij (1968).

Skala Group

The Skala Group (= Skala Horizon) contains, according to Nikiforova and Predtechenskij (1968), three formations (= beds in Russian literature), i.e. in ascending order, the Isakovtsy, Rashkov and Dzwinogorod formations. Later, Tsegelnjuk *et al.* (1983) transferred the Isakovtsy Formation to the Malinovtsy Group.

Koren' *et al.* (1989) also included the lowermost part of the Rashkov Formation (= Prigorodok Formation) in the Malinovtsy Group. The Skala Group is well exposed along the Dnestr, Zbruch and Zhvanchik rivers. Its lithology is mainly limestone, which alternates with dolomites, dolomitic marls, argillites and metabentonite layers. The total thickness of the Skala Group is over 151 m if the Isakovtsy Formation is included (Nikiforova and Predtechenskij 1968) or up to 136 m if one adopts the definition given by Koren' *et al.* (1989).

Isakovtsy Formation. The total thickness of the Isakovtsy Formation ranges from 32–34 m (Nikiforova and Predtechenskij 1968), 5–6 m (Tsegelnjuk *et al.* 1983) or 6–9 m (Koren' *et al.* 1989). In the basal 2–4.5 m massive dolomites occur within thin layers of dolomitic marls and bentonites; higher up, dolomitic marls with bentonites dominate. Desiccation fissures and ripple marks are common in these inner shelf to shoal or lagoon deposits (see Koren' *et al.* 1989, fig. 106). The best exposures are on the left side of Dnestr River and at Okopy village. The fauna consists mainly of brachiopods and ostracodes. The latter may form limestone coquinas. Trilobites and cystoids are scarce, whilst algae are common in the dolomites. The age is generally considered to be upper Ludlow (Koren' *et al.* 1989).

Rashkov Formation. According to Nikiforova and Predtechenskij (1968) the thickness of the Rashkov Formation is *c.* 98 m (a thickness of 170–250 m is given by Tsegelnjuk *et al.* 1983 and of 94–106 m by Koren' *et al.* 1989). The lithologies are nodular dolomite rich in stromatoporoids, bituminous limestone, tuffitic sandstone and bentonite. Desiccation fissures occur in these inner shelf to shallow open shelf deposits (see Koren' *et al.* 1989, fig. 106). A complete section is present on the left bank of the Dnestr River, near Okopy village. The fossil fauna is dominated by stromatoporoids, corals and ostracodes. These may locally be rock-forming. Other important groups are bivalves, nautiloids, bryozoans, brachiopods, trilobites and crinoids. Plant remains are also common. The lower part of the formation has been transferred to the Prigoroduk Formation by some authors (Tsegelnjuk *et al.* 1983; Koren' *et al.* 1989). Age assignments of the Rashkov Formation vary from upper Ludlow (Nikiforova and Predtechenskij 1968; Tsegelnjuk *et al.* 1983) to uppermost Ludlow–lower Přídolí (Koren' *et al.* 1989).

Dzwinogorod Formation. The estimated thickness of the Dzwinogorod Formation is *c.* 19 m according to Nikiforova and Predtechenskij (1968), 29–31 m (Tsegelnjuk *et al.* 1983) or up to 30 m (Koren' *et al.* 1989). The formation consists of grey–green marls with limestone nodules. Bentonites are present in these shallow open shelf to outer shelf (upper part of the formation) deposits (see Koren' *et al.* 1989, fig. 106). Good exposures occur at the Dzwinogorod and Volkovtsy villages. The shelly fauna is rich in stromatoporoids, corals, bivalves, nautiloids, bryozoans, brachiopods, ostracodes, trilobites and crinoids. Plant remains and conodonts have also been described from the formation. The age is considered to be uppermost Ludlow–lower Přídolí by Nikiforova and Predtechenskij (1968), and upper Přídolí by Tsegelnjuk *et al.* (1983) and Koren' *et al.* (1989).

Borshchov Group

The Borshchov Group (= Borshchov Horizon) was subdivided into three formations (= beds in the Russian literature) by Nikiforova and Predtechenskij (1968); in ascending order these are the Tajna, Mitkov and the Bogdanovka formations. The group is the thickest (*c.* 253 m) and most widespread in Podolia. The lithology is characterized by fossiliferous grey argillites, marls and limestones. The type section is at Nichlava River near Borshchov village. A complete section occurs along the Dnestr between Volkovtsy and Zazulinty villages. The Silurian–Devonian boundary is currently correlated with the base of the Borshchov Group (Nikiforova 1977).

Tajna Formation. Nikiforova and Predtechenskij (1968) estimated the thickness of the Tajna Formation to be *c.* 57 m. The lithology consists of rhythmically intermittent marly argillite members, with lenses of limestone followed by limestone and greenish-grey marls. The sequence finishes with dark grey limestone and intercalated argillites. The formation is exposed in two areas at Dnestr and about 80 km north, at Tajna River where the type section is situated. The fauna is rich in corals, bivalves, nautiloids, bryozoans, brachiopods, trilobites and crinoids; graptolites and conodonts have also been described from the formation. The age is generally believed to be lower Lochkovian.

Mitkov Formation. The Mitkov Formation is estimated to be *c.* 126 m thick (Nikiforova and Predtechenskij 1968). The lithology is grey calcareous argillite or marly shale with bun-shaped limestone concretions. The Mitkov Formation crops out along the Dnestr River from the city of Melnitsa-Podolskaya to Bogdanovka

village and along the Nichlava River. Brachiopods are common and sometimes form coquinas. Other elements of the fauna include corals, bivalves, nautiloids, bryozoans, trilobites, ostracodes, crinoids, graptolites and fish remains; plant remains and conodonts have also been described. The age is considered to be lower Lochkovian.

Bogdanovka Formation. Nikiforova and Predtechenskij (1968) determined the thickness of the Bogdanovka Formation to be *c.* 69 m. The lithology is mainly thin-bedded limestone intercalated with argillaceous marls. Brachiopods, tentaculitids and bivalves are numerous and form coquina limestones. Other common shelly fossil groups are corals and nautiloids; conodonts have also been described. Exposures are present along the Dnestr for a short distance between the Bogdanovka and Zazulinty villages. The upper part can also be observed at Bilche Zolotoe village on the Seret River. The age of the formation is considered to be lower Lochkovian.

Chortkov Group

According to Nikiforova and Predtechenskij (1968) the total thickness of the Chortkov Group is *c.* 135 m. The group is characterized by thin beds of alternating dark grey limestone and greenish-grey argillite. Ostracodes, bivalves and tentaculitids are common and form coquinas. Other shelly fossil groups represented are bryozoans, orthocones, brachiopods and corals. Fish remains and conodonts are also common. The Chortkov Group crops out extensively along the Dnestr, the Seret and the Dupa rivers. The type section is at Seret River, north of Zvinyach city and the age is believed to be lower Lochkovian.

Ivane Group

The Ivane Group, with a total thickness of *c.* 126 m (Nikiforova and Predtechenskij 1968), can be divided into four lithological units. A lower unit (about 47 m thick) consists of grey argillites alternating with red siltstones and limestone concretions. This is overlain by a unit, *c.* 42 m thick, containing grey siltstones alternating with limestones. The third unit (*c.* 22 m thick) is characterized by bioturbated grey to yellowish-green siltstone, and the uppermost unit (*c.* 15 m thick) consists of red siltstone and limestone alternating with grey, bioturbated siltstone. The Ivane Group crops out along the Dnestr River from Dobrovlyany to Ustechko villages, and along the Seret, Belaya and Perejma rivers. The type section is located near the Ivane Zolotoe village. Except for the ostracodes, the fossil faunas are similar to those of the underlying Chortkov Group. The faunas are dominated by corals, bivalves, brachiopods, nautiloids (locally forming a coquina), tentaculitids, crinoids and fish remains. The age is believed to be upper Lochkovian.

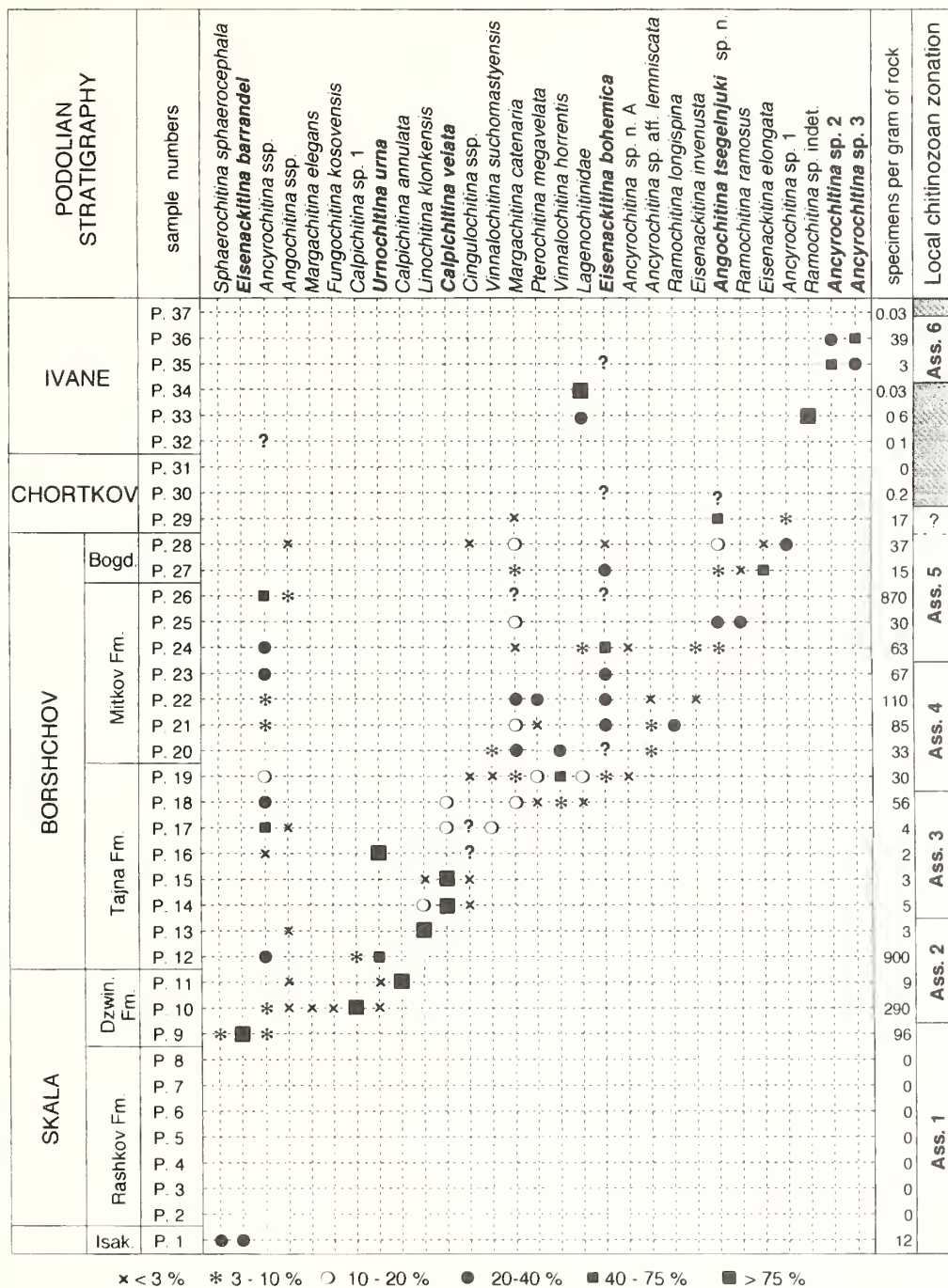
Dnestr Supergroup

The total thickness of the Dnestr Supergroup is estimated as *c.* 350 m (Nikiforova and Predtechenskij 1968). The lithology is exclusively continental red terrigenous sandstones, siltstones and mudstones. Desiccation fissures and ripple marks are common. The Supergroup crops out along the Dnestr River, from Zaleshchiki city to Ustechko village, and along the Dupa, Dzhurin and other rivers. Numerous fish remains are present in the basal part, and based on these, the age is at the Lochkovian–Pragian transition (Nikiforova and Predtechenskij 1968; Karatajute-Talimaa 1978).

METHODS, AND LOCALITIES STUDIED

Thirty-seven samples from nine localities exposing a marine sequence of Upper Silurian–Lower Devonian age have been investigated for chitinozoans. Standard methods for laboratory and electron microscope studies (Paris 1981) were used. The locality numbers referred to are those of Nikiforova and Predtechenskij (1968). It should be noted that our sparsely distributed samples do not allow a detailed study of the actual sequence; such a study would require hundreds of closely collected samples.

Near Zhwanetz village (locality 83, river-bank exposure on the left side of the Dnestr about 500 m above the bridge at Zhwanetz village), approximately 12 m of the Grinchuk Formation of the Malinovtsy Group is overlain by the basal 12 m of the Isakovtsy Formation. Sample P.1 was taken at the base of the Isakovtsy Formation.



TEXT-FIG. 2. Distribution, abundance and local biozonation of the chitinozoans in the Upper Silurian and Lower Devonian sequences of the Dnestr valley, Podolia, Ukraine. Index taxa of the local chitinozoan zonation are in bold. Local stratigraphical terminology from Nikiforova and Predtechenskiy (1968) and Koren' *et al.* (1989).

At Trubchin village (locality 38, exposure on the left side of the Dnestr about 400 m below Trubchin village), typical beds of the middle part of the Rashkov Formation are exposed. Seven samples (P.2 to P.8) were collected in the lower and middle part of the section (Text-fig. 3). All were barren (Text-fig. 2).

At Volkovtsy village (locality 64, exposure at a gully near a church at Volkovtsy village), at the left side and at the base of the gully, nearly 7 m of the upper Dzwinogorod Formation are exposed; three samples were collected from this part (P.9 to P.11). These beds are overlain by more than 20 m of the Tajna Formation. Four samples (P.12 to P.15) were collected in the basal part of the Tajna Formation, and one sample (P.16) from higher up in the section (Text-fig. 3).

Close to Chudkovtsy village (locality 48, exposure at the left side of the Dnestr River about 500 m above Chudkovtsy village; Text-fig. 1), the upper Tajna Formation is exposed in the lower part of the section and about 20 m of the Mitkov Formation is visible above this. The Devonian beds are overlain here by Cenomanian limestones. Three samples (P.17, P.18 and P.19) were collected from the Tajna Formation, at the base and in the top of the exposed sequence, and one sample (P.20) in the basal part of the overlying Mitkov Formation (Text-fig. 3).

At Mikhalkov village (locality 92, exposure on the left side of the Nichlava River opposite the mill at Ustje village; Text-fig. 1), over 40 m of the middle Mitkov Formation are exposed. Samples were taken at the base (P.21) and the middle part (P.22) of the section (Text-fig. 3).

Near Bogdanovka village (locality 56, exposure in a creek on the left side of Dnestr River, about 1 km below the Bogdanovka village; Text-fig. 1), the upper part of the Mitkov Formation and the lower part of the overlying Bogdanovka Formation are exposed. Four samples (P.23 to P.26) were collected in the Mitkov Formation, and two samples (P.27 and P.28) in the lower Bogdanovka Formation (Text-fig. 3).

Near Gorodok village (locality 81, road-cut on the left side of the Seret River along the road between Kulakovtsy and Gorodok villages), the middle part of the Chortkov Group is exposed. Three samples (P.29–P.31) were collected in the lower segment of this exposure (Text-fig. 3).

Close to Dosrovlyany village (locality 73, exposure on the left side of the Dnestr about 500 m below Dobrovlyany village), the lower part of the Ivane Group is present. Five samples (P.32 to P.36) were collected from the middle and upper part of the section (Text-fig. 3).

At Ivane-Zolotoe village (locality 76, exposure on the left side of the Dnestr about 500 m below Ivane-Zolotoe village), c. 36 m of the upper Ivane Group and nearly 50 m of the lower Dnestr Supergroup crop out in rain-rills of a steep slope in the valley. One sample (P.37) was collected at the top of the Ivane Group (Text-fig. 3).

EXPLANATION OF PLATE I

Chitinozoans from Tajna and Mitkov formations, Podolia, Ukraine.

Figs 1, 6. *Calpichitina annulata* (Paris and Laufeld, in Paris *et al.*, 1981). 1, P.11, IGR 58706 (O.40/4); oblique apertural view; $\times 400$. 2, P.11, IGR 58706 (Q.43); detail of the operculum with turned-up borders; the circular perforation is due to parasite boring; $\times 750$.

Figs 2–3, 8. *Vinnalochitina suchomastiensis* (Paris and Laufeld, in Paris *et al.*, 1981). 2, P.17, IGR 58717 (M.40); lateral view of a specimen in full relief; $\times 400$. 3, P.20, IGR 58723 (P.39/4); lateral view of a partially flattened specimen; $\times 400$. 8, P.20, IGR 58723 (L.40/3); anteapertural oblique view showing the scar, and the spiny ornamentation fading away toward the apex; $\times 400$.

Fig. 4. *Cingulochitina wronai* Paris and Kříž, 1984; P.14, IGR 58712 (Q.39); isolated vesicle with a very short carina; $\times 400$.

Figs 5, 11. *Vinnalochitina? horrentis* (Jaglin, 1985). 5, P.19, IGR 58721 (U.43/3); chain of three flattened vesicles; $\times 400$. 11, P.20, IGR 58723 (P.40/4); apertural oblique view of an isolated specimen showing peculiar ornamentation; $\times 500$.

Figs 7, 9. *Calpichitina velata* (Wrona, 1980). P.14, IGR 58712. 7, (R.39); apertural view of a flattened vesicle; $\times 400$. 9, (O.36); apertural view of a specimen with well-developed outer-layer foldings; $\times 400$.

Fig. 10. *Cingulochitina* ex. gr. *ervensis* (Paris, 1979); P.19, IGR 58721 (N.41/4); the partly collapsed flanks slightly modify the outline of these specimens; $\times 350$.

Fig. 12. *Urnochitina urna* (Eisenack, 1934); P.12, IGR 58708 (N.41/3); note the operculum still fixed to the succeeding vesicle; $\times 300$.

Fig. 13. *Linochitina klonkensis* (Paris and Laufeld, in Paris *et al.*, 1981); P.13, IGR 58710 (P.38); note the fragments of collarette remaining attached to the margin of the upper vesicle and simulating a carina; $\times 300$.



CHITINOZOAN BIOSTRATIGRAPHY AND CHRONOSTRATIGRAPHY

The abundance of chitinozoans in the samples is highly variable (Text-fig. 2) and ranges from 0.03 specimens per gramme of rock (e.g. sample P. 34) up to 900 specimens per gram of rock (e.g. samples P. 12 and P. 26). The distribution and the abundance of these organic microfossils seem to be influenced by both the lithology and the environment. The lagoonal to inner shelf deposits of the Rashkov Formation are virtually barren while the outer shelf deposits (e.g. dark bituminous limestones of the Tajna or Mitkov formations) yield rich and highly diversified chitinozoan assemblages (Text-fig. 2). The reddish lithologies of the Ivane Group contain few chitinozoans but abundant organic tubes (Pl. 2, figs 4, 7–9) reminiscent of some of the terrestrial plant microfossils reported by Wellman and Richardson (1993) from the Silurian of Scotland.

Local chitinozoan biozonation (Text-fig. 2)

Six chitinozoan assemblages, corresponding to interval biozones between the first occurrence of two successive index taxa, have been identified. The term 'assemblage' is used instead of the more formal 'biozone' because the sampling is too sparse to document precisely the actual range of the recorded taxa. Most of the index species have been selected because they allow correlation with the Upper Silurian and Lower Devonian international stratotypes defined in Bohemia.

Assemblage 1. This corresponds to the total range of *Eisenackitina barrandei* in the investigated material. This index species is only recorded in the lower part of the Isakovtsy Formation (poorly preserved individuals in sample P. 1) and in the upper middle part of the Dzwynogorod Formation (sample P. 9; 80 per cent. of the recovered chitinozoans); the analysed samples from the Rashkov Formation were barren. The associated species are *Sphaerochitina sphaerocephala* (35 per cent. of the population recorded in sample P. 1), *Cingulochitina* sp. indet., a few specimens of *Ancyrochitina* sp. aff. *primitiva* and *Eisenackitina*, e.g. *E. intermedia*.

Assemblage 2. This assemblage commences with the first occurrence of *Urnochitina urna* in sample P. 10 (less than 3 per cent. of the population). This material was collected a few tens of millimetres below the top of the

EXPLANATION OF PLATE 2

Early Lochkovian chitinozoans from the upper part of the Tajna Formation (figs 6, 10a–b) and from the lower part of the Mitkov Formation (figs 1–3, 5 and 12) of Podolia, Ukraine. A few organic tubes from the Lower Devonian of Podolia are also illustrated.

Fig. 1. *Ramochitina* sp. aff. *jouannensis* (Paris, 1976); P. 21, IGR 58727, (P. 41/3); full relief specimen in lateral view; $\times 350$.

Figs 2–3. *Ramochitina longispina* (Wrona, 1980); P. 21, IGR 58727, 2, (S. 39/4); $\times 350$. 3, (S. 42/3); $\times 350$.

Fig. 4. Organic 'tube' with a vermiculate outer surface, P. 32, IGR 58745, (Q. 40/2); lower part of the Ivane Group; $\times 600$.

Fig. 5. *Eisenackitina invenusta* Wrona, 1980; P. 22, IGR 58728, (N. 38/4); specimen with partly collapsed flanks; $\times 300$.

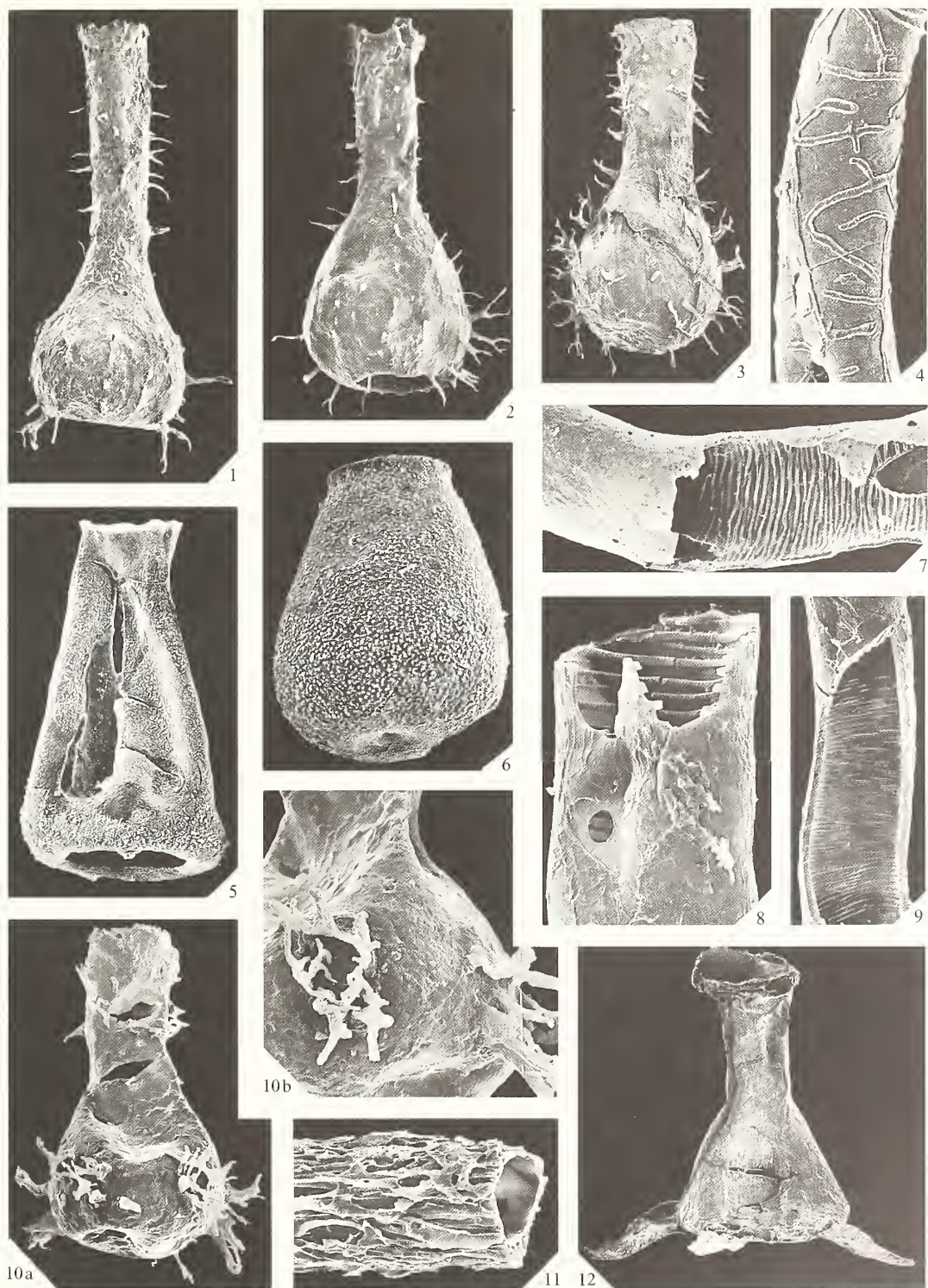
Fig. 6. *Eisenackitina bohemica* (Eisenack, 1934); P. 19, IGR 58721, (R. 43); $\times 250$; note the slightly depressed anteapectural scar.

Figs 7–9. *Porcatitubulus?* sp. Burgess and Edwards, 1991. Organic 'tubes' showing a smooth outer surface and an annulate inner surface. 7, P. 32, IGR 58745, (O. 36); base of the Ivane Group; $\times 700$. 8, P. 13, IGR 58710, (Q. 38/3); note the perforation of the tube wall of this specimen; lower part of the Tajna Formation; $\times 750$. 9, P. 19, IGR 58721, (S. 41/2); top of the Tajna Formation; $\times 500$.

Fig. 10a–b. *Ancyrochitina* sp. nov. A; P. 19, IGR 58721, (R. 39/4). a, specimen in lateral view; $\times 400$. b, detail of the very diagnostic processes of this new species; $\times 750$.

Fig. 11. Organic 'tube' with large, irregular, longitudinal ridges on its outer surface; P. 13, IGR 58721, (M. 40); lower part of the Tajna Formation; $\times 500$.

Fig. 12. *Ancyrochitina* cf. *lemniscata* Wrona, 1980; P. 21, IGR 58725, (R. 38/1); note the very wide processes; $\times 250$.



Dzwinogorod Formation in the Vokovtsy section (= section 64 in Nikiforova and Predtechenskij 1968). The assemblage extends up to sample P.14 but *U. urna* ranges at least into the lowest quarter of the Tajna Formation as the species is still present in sample P.16 (= bed 12 in section 64 of Nikiforova and Predtechenskij 1968). The distribution of *U. urna* is discontinuous in the lower part of the Tajna Formation. It is worth noting the occurrence of a few *Margachitina elegans* in sample P.10. This species is well-known from the middle part of the Přídolí in northern Gondwana regions (Boumendjel 1987; Verniers *et al.* 1995). Some *Fungochitina* forms, including typical *Fungochitina kosovensis*, are also recorded in sample P.10, which is dominated by *Calpichitina* sp. 1 (85 per cent. of the population).

Assemblage 3. This begins in the lower part of the Tajna Formation with the first occurrence of *Calpichitina velata* in sample P.14. This species extends over about 50 m, i.e. almost all of the Tajna Formation. Its last record is in sample P.18, which was collected a few metres below the Tajna–Mitkov boundary. Consequently, *C. velata* coexisted with both *U. urna* and with *Calpichitina annulata*. Until now, this latter species has only been recorded in the highest Přídolí beds of the Klonk section (Lochkovian GSSP) in Bohemia (Paris 1981; Paris *et al.* 1981). The highest specimens of *C. velata* coexisted with the first specimens of *Pterochitina megavelata* and *Margachitina catenaria*, two taxa well represented in the succeeding chitinozoan assemblage.

Assemblage 4. This assemblage begins at the appearance of *Eisenackitina bohemica* in sample P.19 i.e. 0.25 m below the top of the Tajna Formation (upper part of bed 5 of Chudkovtsy section in Nikiforova and Predtechenskij 1968). *E. bohemica* is represented by only a few individuals in sample P.19, but this important species dominates the chitinozoan assemblages higher up in the Mitkov Formation (e.g. 48 per cent. in sample P.23 and 54 per cent. in sample P.24). The greatest chitinozoan diversity is in the lower part of the Mitkov Formation where *P. megavelata* and *M. catenaria* are also well represented (respectively 26 per cent. and 32 per cent. of the chitinozoans recorded in P.22). Other species seem to have a more restricted distribution e.g. *Ancyrochitina* sp. nov. A (sample P.19) and *Ramochitina longispina* (sample P.21).

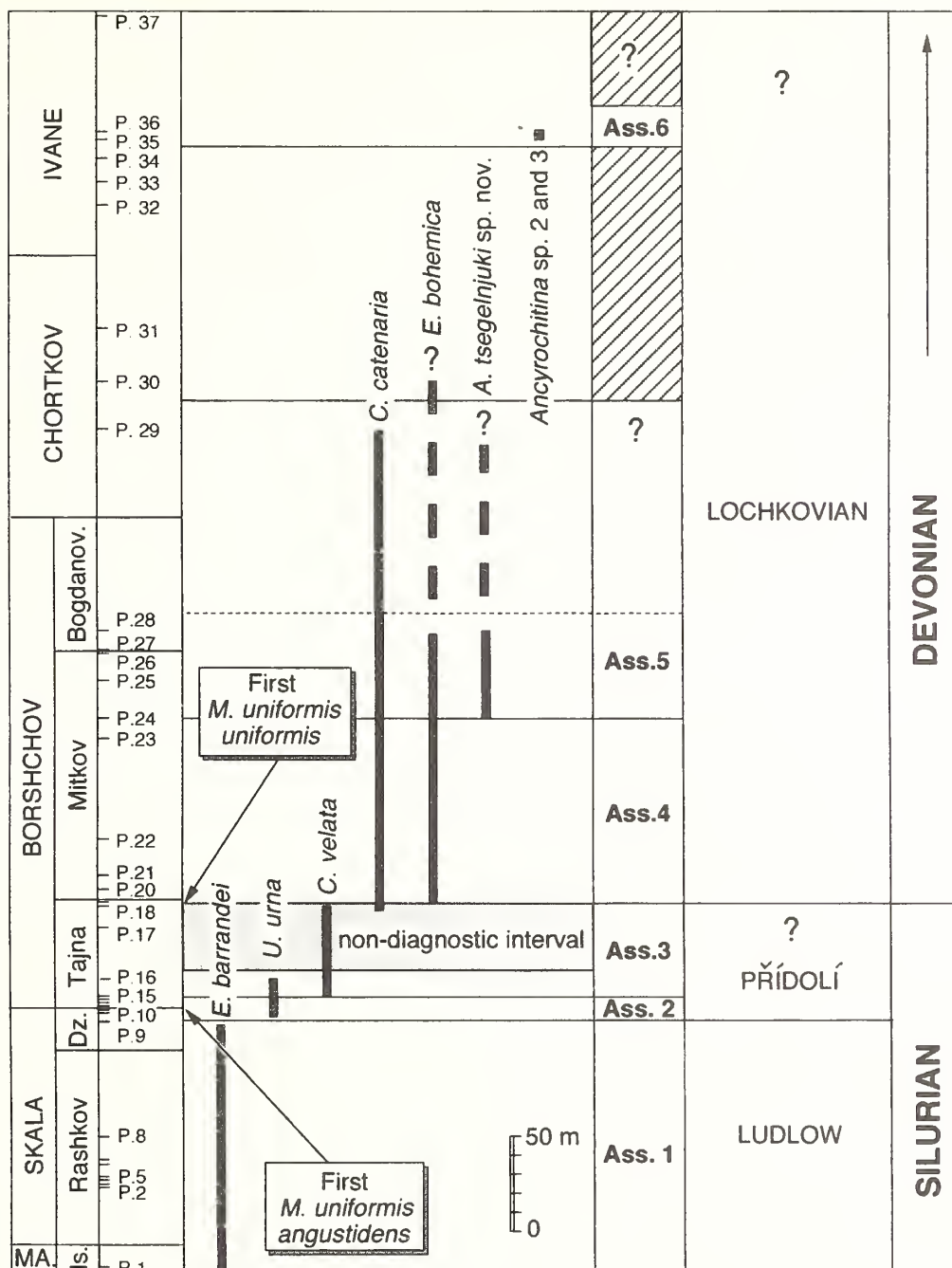
Assemblage 5. This corresponds to the total range of *Angochitina tsegehnjuki* sp. nov. from sample P.24 to sample P.28, and possibly up to P.29, depending on the taxonomic status of a closely related form tentatively called here *A. tsegehnjuki* sp. nov.? This assemblage, therefore, characterizes the upper part of the Mitkov Formation, the lower part of the Bogdanovka Formation and possibly extends into the lower part of the Chortkov Group. The index species coexisted with the last representatives of *Margachitina catenaria* and *E. bohemica*. *E. elongata*, a stratigraphically more restricted taxon, is abundant in sample P.27, at the base of the Bogdanovka Formation.

Assemblage 6. This assemblage is limited to samples P.35 and P.36 in the middle part of the Ivane Group. It is characterized by the occurrence of two distinctive forms: *Ancyrochitina* sp. 2 (Pl. 4, figs 3, 6, 9) and *Ancyrochitina* sp. 3 (Pl. 4, figs 1–2). A poorly preserved *Eisenackitina* form might belong to *E. bohemica*. The chitinozoans recovered from the upper part of the Bogdanovka Formation and from the lower part of the Ivane Group are too sparse and too poorly preserved to document convincingly any biozonation.

Chronostratigraphical assignment

Most of the index taxa selected here are regarded as good chronostratigraphical markers as their respective ranges are well constrained with respect to the Upper Silurian and Lower Devonian GSSP (Paris *et al.* 1981; Chlupáč *et al.* 1985; Kříž *et al.* 1986; Verniers *et al.* 1995; Paris 1996).

In Bohemia, *E. barrandei*, the index taxon of our Assemblage 1 in Podolia, is a typical Late Ludlow chitinozoan species (Paris and Kříž 1984). In the Prague basin, it is abundant in all sections exposing the Ludlow–Přídolí boundary (Kříž *et al.* 1986). It usually disappears at the top of the Ludlow, but, in some localities (e.g. Požáří section, where the GSSP of the Přídolí is defined), *E. barrandei* extends a few hundred millimetres above the base of the Přídolí, i.e. above the first occurrence of *Monograptus parultimus* (see Kříž *et al.* 1986, fig. 7). In Podolia, this Assemblage 1, ranging from the Isakovtsy Formation to the upper two-thirds of the Dzwinogorod Formation, suggests that the Ludlow–Přídolí boundary is situated within the Dzwinogorod Formation, in all likelihood in its middle part. This age assignment is supported by the first occurrence of *U. urna* at the top of the Dzwinogorod Formation; in Bohemia, this world-wide chitinozoan index species for the Přídolí (Verniers *et al.* 1995) appears a few tens of millimetres above the first *M. parultimus* (Kříž *et al.* 1986). This chronostratigraphical assignment contradicts earlier stratigraphical conclusions,



TEXT-FIG. 3. Range of selected chitinozoan taxa and chronostratigraphical assignment based on chitinozoan evidence. Lithological units and thicknesses from Nikiforova and Predtechenskij (1968) and Koren' *et al.* (1989). (Hatching: barren interval. Abbreviations: Ass. = assemblage; MA. = Malinovtsy; Is. = Isakovtsy; Dz. = Dzwinogorod; Bogdanov. = Bogdanovka).

based on the local range of the conodonts *Ozarkodina remscheidensis eosteinhornensis* and *O. crista* which placed the Ludlow–Přídolí boundary in the lower part of the underlying Rashkov Formation (Abushik *et al.* 1985). However, it should be stressed that in Bohemia *O. remscheidensis eosteinhornensis* and *O. crista* occur within strata situated several metres below the base of the Přídolí (Kříž *et al.* 1986). Therefore, in our opinion, the occurrence of these two conodonts in the Podolian sections is not sufficient to locate precisely the Ludlow–Přídolí boundary. Ostracodes are of limited use because almost none of the Podolian taxa is reported from the Ludlow and Přídolí in Bohemia (Kříž *et al.* 1986). A bed-by-bed study of the chitinozoans from the highest ten metres of the Dzwinogorod Formation in the Volkovtsy section, would certainly pin-point more accurately the location of the Ludlow–Přídolí boundary in Podolia.

Based on chitinozoan data, especially on the total range of *U. urna*, the Přídolí appears to extend at least 15 m into the lower part of the Tajna Formation (Text-fig. 3) and possibly higher. There is an interval of 20 m which was not investigated within the 40 m thick sequence separating the last recorded *U. urna* from the appearance of *E. bohémica*, a diagnostic chitinozoan species for the Lochkovian (Paris 1981).

The chronostratigraphical conclusion concerning the Přídolí–Lochkovian boundary i.e. the Silurian–Devonian boundary, based on chitinozoan evidence, is again in disagreement with the age assignments proposed by previous workers. In particular, the chitinozoan evidence is in conflict with the conclusion of graptolite experts who have drawn the Silurian–Devonian boundary at the base of the Tajna Formation because *Monograptus uniformis angustidens* has its first occurrence in the basal bed of this unit (Koren' 1968). However, by definition, the base of the Devonian, and therefore of the Lochkovian, coincides with the first occurrence of *Monograptus uniformis uniformis* (McLaren 1977; Holland 1985), a closely related subspecies which has its first appearance much higher in the Podolian succession, i.e. three metres below the base of the Mitkov Formation in the Chudkovtsy section (Nikiforova and Predtechenskij 1968). In Bohemia, these two graptolite subspecies appear together in bed 20 of the Klonk section (GSSP of the base of the Devonian). Moreover, in Klonk, *Calpichitina annulata* is restricted to beds 18–20, i.e. very close to the first occurrence of *M. u. angustidens* in bed 20. A similar situation is noted in Podolia where *C. annulata* is only recorded in sample P. 11, just below the first report of *M. u. angustidens* in the Chudkovtsy section (Nikiforova and Predtechenskij 1968). On the other hand, in both localities, *E. bohémica* has its first occurrence a very short distance above the appearance of *M. u. uniformis*. However, there is a major difference between these two localities: in the Chudkovtsy section a 54 m thick sequence separated the first occurrence of each graptolite subspecies, whereas in Klonk they occur in the same bed. This could be explained either by a more complete sedimentological record in Podolia or by

EXPLANATION OF PLATE 3

Early Lochkovian chitinozoans from the Mitkov Formation of Podolia, Ukraine.

Figs 1–2. *Margachitina catenaria* Obut, 1973. 1, P. 22, IGR 58728, (K.37/4); lateral view of a chain of four vesicles; $\times 300$. 2, P. 25, IGR 58733, (L.38/4); note the thick peduncle and the horizontal ribs on these specimens; $\times 300$.

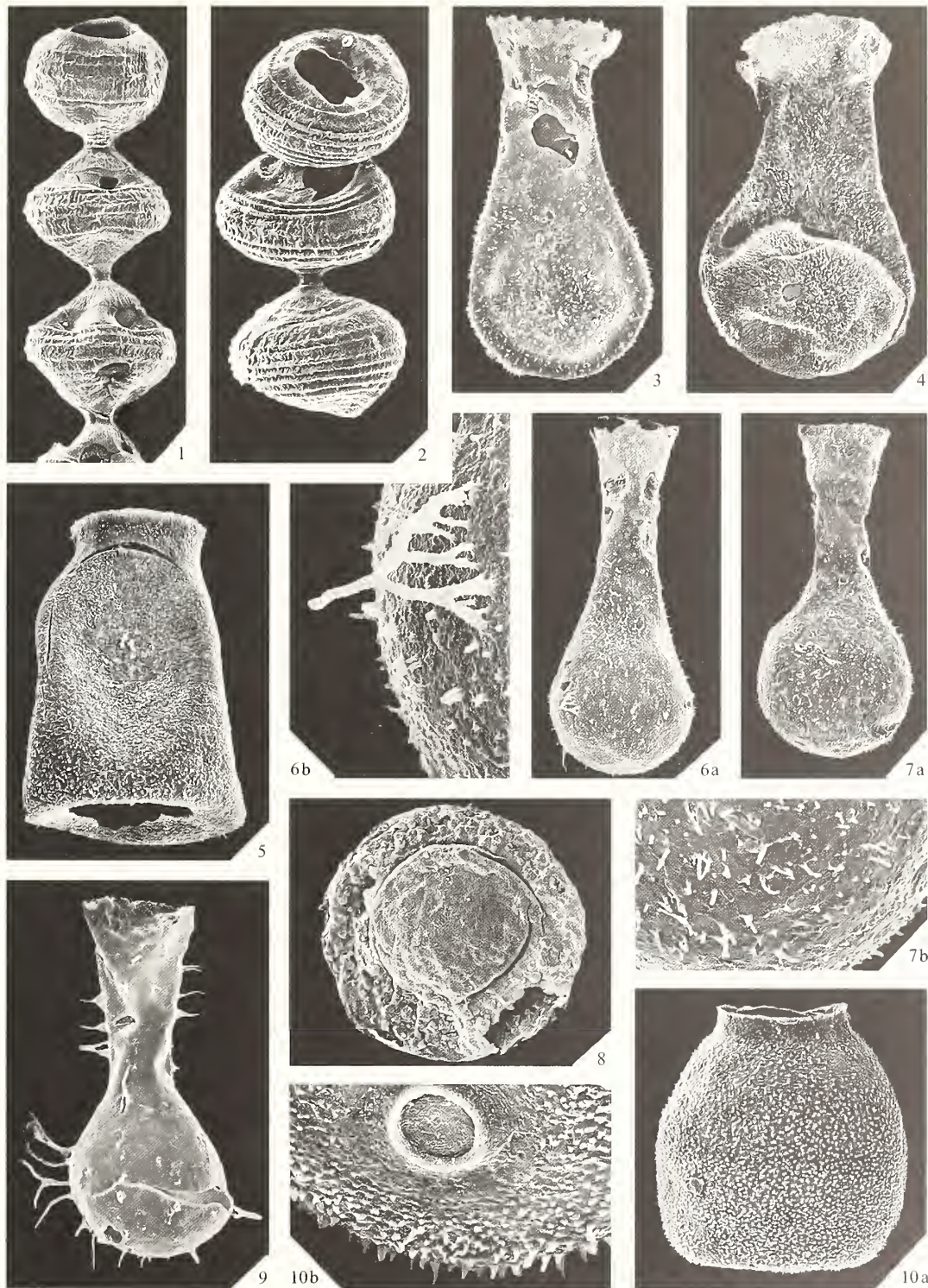
Figs 3–4, 6a–b, 7a–b. *Angochitina tsegehujuki* sp. nov.; P. 25, IGR 58733. 3, (N.42/1); lateral view of flattened paratype; $\times 300$. 4, (L.40/3); lateral view of flattened paratype with a densely distributed spiny ornamentation; $\times 300$. 6, (O.41), holotype. a, lateral view; $\times 300$, b, detail of a multirooted spine; $\times 2000$. 7, (M.39/1); atypical paratype with a fairly rounded chamber. a, $\times 300$. b, detail of the spiny ornamentation; $\times 1000$.

Fig. 5. *Eisenackitina invenusta* Wrona, 1980; P. 24, IGR 58731, (P.39); $\times 350$.

Fig. 8. *Pterochitina megavelata* (nomen nudum, in Boumendjel 1987); P. 22, IGR 58728, (L.36/1); anteapertural view; $\times 300$.

Fig. 9. *Ramochitina ramosus* (Paris, 1976); P. 25, IGR 58733, (P.41/1); $\times 300$.

Fig. 10a–b. *Eisenackitina bohémica* (Eisenack, 1934), P. 22, IGR 58728. a, (Q.38/1); lateral view of a stubby specimen; $\times 250$. b, detail of the mucron and of the spiny ornamentation on a tilted vesicle; $\times 750$.



the diachronous occurrence of some chitinozoan and graptolite species. If one adopts the first hypothesis, bed 20 in the Klonk section would represent a condensed or a disturbed deposit. In the second hypothesis, both *M. u. uniformis* and *E. bohémica* appeared later in Podolia whereas *U. urna* survived longer there than in Bohemia. Another alternative explanation may be that *M. u. angustidens* appeared earlier in Podolia than in Bohemia. We favour the sedimentological explanation because an obvious change in lithology, with a local erosional pattern, can be observed at precisely the Silurian–Devonian boundary in bed 20 of the Klonk section (see fig. 3 in Hladil 1991). Moreover, a similar biostratigraphical discrepancy is observed in Poland (Wrona 1980).

Assemblage 3, containing *Calpichitina velata*, is of more limited use for a high resolution age assignment as this taxon is also recorded in the uppermost Přídolí–lowermost Lochkovian beds of the Karlštejn section in Bohemia (= chitinozoan indet. n. gen.? n. sp. in Paris *et al.* 1981) and in the Bostovian–Lower Ciepeliavian (= Lochkovian) of well Strzelce IG.2 in Poland (Wrona 1980). The species is also reported in the Lochkovian of Artois, northern France (Paris 1986) and in the Lochkovian and lower Pragian of Australia (Winchester-Seeto 1993).

Assemblage 4, corresponding to the lower part of the total range of *E. bohémica* and of *M. catenaria*, is typically of early Lochkovian age. Based on the known range of *E. bohémica* (Paris 1981, 1995; Chlupáč *et al.* 1985), the topmost Tajna Formation, the whole Mitkov Formation and at least the lower part of the Bogdanovka Formation are of Lochkovian age.

Assemblage 5, despite the fact that it corresponds to the total range of a new chitinozoan species i.e. *Angochitina tsegehnjuki*, is dated by the upper half of the *E. bohémica* total range biozone and also by the occurrence of *E. elongata*, a taxon already recorded in the upper Lochkovian in Bohemia (e.g. bed No. 5 of the Trebotov section; bed 10/11 in the Kosor section; Paris in Chlupáč *et al.* 1985). The Late Silurian–Early Devonian *Margachitina* species usually display an evolutionary trend of progressive thinning of the peduncle (Paris 1981). This is illustrated by the lineage *M. crassipes* (late Přídolí), *M. catenaria* (early Lochkovian) and *M. tenuipes* (late Lochkovian–early Pragian). The youngest individuals recorded in Podolia (sample P.29, from the lower part of the Chortkov Group) still belong to *M. catenaria*. Therefore, it is concluded that the base of the Chortkov Group is still Lochkovian.

In assemblage 6, from the Ivane Group, the two dominant forms *Ancyrochitina* sp. 2 and *Ancyrochitina* sp. 3 are not, as yet, useful for chronostratigraphical purposes. However, the

EXPLANATION OF PLATE 4

Lochkovian chitinozoans from the Bogdanovka Formation (figs 5a–b, 8a–b), and from the Chortkov (figs 10a–b) and Ivane groups (figs 1–4, 6–7, 9), Podolia, Ukraine.

Figs 1–2. *Ancyrochitina* sp. 3; P.36, IGR 58752. 1, (M.40/2); damaged specimen with short spines covering the entire vesicle; $\times 400$. 2, (M.39/3); detail of the spiny wall of another specimen; $\times 1000$.

Fig. 3. *Ancyrochitina* sp. 2; P.35, IGR 58750, (N.36/3); specimen with collapsed flanks; $\times 400$.

Fig. 4. *Ramochitina* sp. indet.; P.33, IGR 58747, (R.39/3); $\times 400$.

Fig. 5a–b. *Eisenackitina bohémica* (Eisenack, 1934); P.27, IGR 58738 (N.35/3). a, flattened specimen in lateral view; $\times 250$. b, detail of the anteapertural scar, clearly without perforation; $\times 1000$.

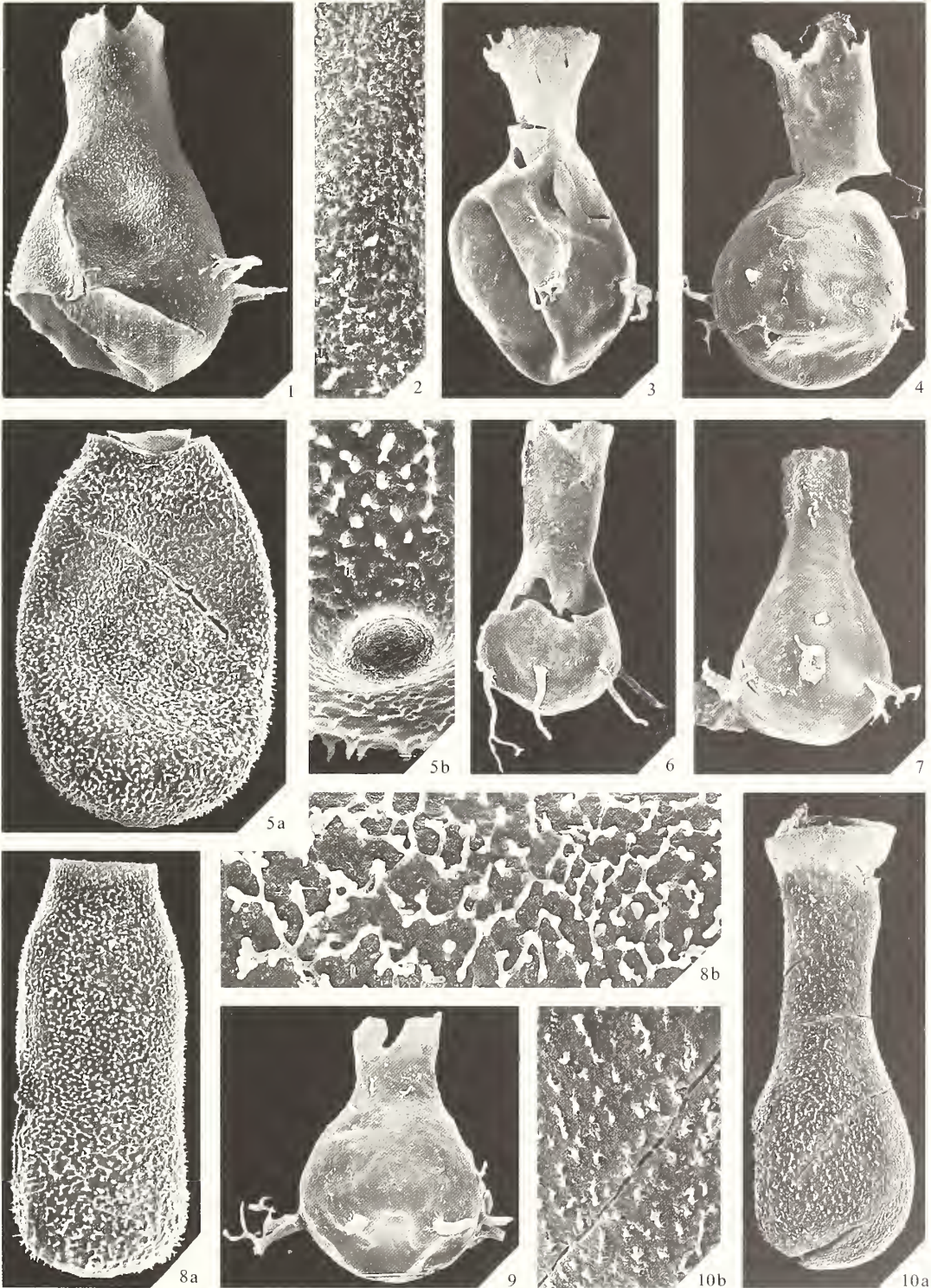
Fig. 6. *Ancyrochitina* sp. 2; P.35, IGR 58750, (P.33/1); note the granulose ornamentation of the neck; $\times 300$.

Fig. 7. *Ancyrochitina* sp. indet.; P.35, IGR 58750, (P.33/1); note the granulose ornamentation of the neck; $\times 300$.

Fig. 8a–b. *Eisenackitina bohémica* (Eisenack, 1934); P.27, IGR 58738, (P.35/2). a, very slender specimen with a silhouette recalling that of *E. elongata* Eisenack, 1972; $\times 250$. b, detail of the peculiar ornamentation with ridges joining the spines; $\times 1000$.

Fig. 9. *Ancyrochitina* sp. 2; P.35, IGR 58750, (Q.35/3); note the multibranched processes of this specimen which has a partly broken neck; $\times 400$.

Fig. 10a–b. *Angochitina tsegehnjuki* sp. nov.?; P.29, IGR 58742, (M.41/4). a, large specimen in lateral view; $\times 300$. b, detail of the short spiny ornamentation of the chamber; note the presence of some multirooted spines and a flaring collarete; $\times 1000$.



occurrence of a very poorly preserved specimen of *Eisenackitina* in sample P.35 would suggest that the Ivane Group should still be Lochkovian. The nearshore environment which prevailed during the deposition of the Ivane sediments was too unfavourable for chitinozoan preservation to permit accurate biostratigraphical conclusions based only on chitinozoan evidence. However, based on the few miospore assemblages illustrated by Arkhangelskaya (1980), both the Chortkov and Ivane groups contain forms belonging to the lower and middle part of the *micrornatus-newportensis* spore Zone (Richardson *et al.* 1981, 1984).

Stratigraphical conclusions

The changes we propose in the present study for the position of some chronostratigraphical limits in the Upper Silurian–Lower Devonian sequences of Podolia are documented by direct correlation with the international stratotypes of Bohemia. These modifications in the local chronostratigraphy have important consequences for other groups reported from Podolian localities, such as pteraspids (Karatajute-Talimaa 1978; Blicek 1984) and spores (Arkhangelskaya 1980, Steemans 1989) as these fossils have been used frequently for indirect dating of non-marine strata (e.g. Richardson *et al.* 1981, 1984). So far, the Silurian–Devonian sequence of Podolia seems to provide one of the most complete records of upper Přidolí–lower Lochkovian deposits yielding chitinozoans as well as acritarchs and miospores. Therefore, this succession should be used for a high resolution biostratigraphical study, integrating detailed sedimentological investigation and a bed-by-bed record of palynomorph groups and other fossils of stratigraphical value. Such data should serve as a key for accurate correlation of marine and non-marine deposits close to the Silurian–Devonian boundary.

SYSTEMATIC PALAEONTOLOGY

Only one new species and one form kept in open nomenclature are described briefly here. The material is deposited in the 'collections de l'Institut de Géologie de Rennes' (IGR) under the numbers 58707 to 58755. England–Finder co-ordinates are used to locate the specimens on the palynological slides. The morphological terminology is that discussed by Paris (1981) with some modifications and additions. The following symbols are used: L (total length of the vesicle), l (length of the chamber), D (maximum diameter of the chamber), d (diameter of the neck), dcoll. (diameter of the collarete). The measurements were made on full relief specimens.

Order PROSOMATIFERA Eisenack, 1972

Family LAGENOCHITINIDAE Eisenack, 1931 emend Paris, 1981

Subfamily ANGOCHITININAE Paris, 1981

Genus ANGOCHITINA Eisenack, 1931

Type species. Angochitina echinata Eisenack, 1931.

Angochitina tsegelnjuki sp. nov.

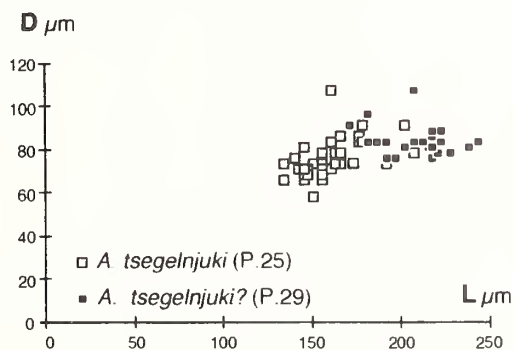
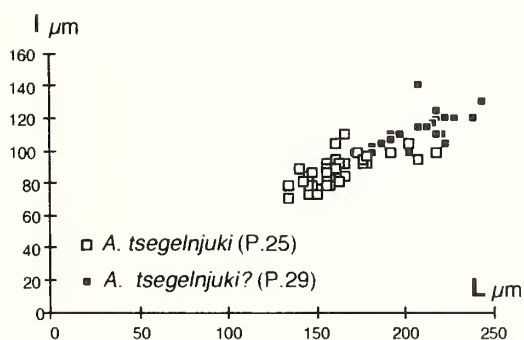
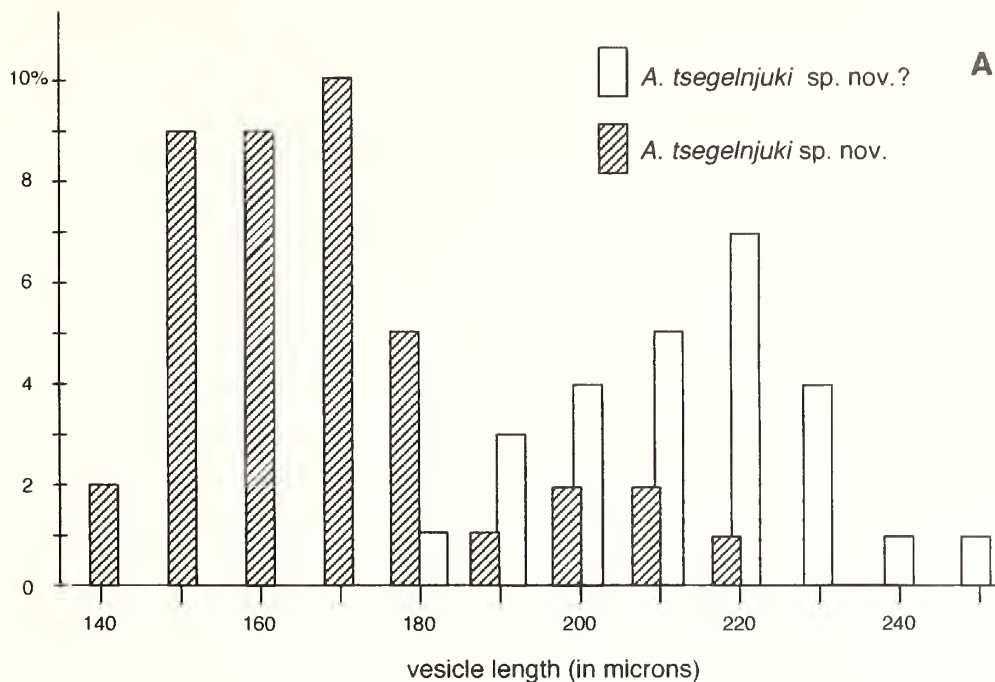
Plate 3, figures 3–4, 6a–b, 7a–b

Derivation of name. To honour Professor Tsegelnjuk (University of Kiev, Ukraine) for his work on Silurian chitinozoans from Podolia.

Holotype. IGR 58753 (O.41) (Pl. 3, fig. 6a); Upper Mitkov Formation, 15 m below its top, Lochkovian; Bogdanovka village, exposure in a creek on the left side of the Dnestr River.

Paratypes. IGR 58753 (N.42/1) (Pl. 3, fig. 3); IGR 58753 (L.40/3) (Pl. 3, fig. 4), IGR 58753 (M.39/1) (Pl. 3, fig. 7a).

Material. Over 200 specimens, both flattened and in full relief, recorded in samples P.24–P.28.



B

C

TEXT-FIG. 4. A, histogram of the variation of the vesicle length (L) in *Angochitina tsegelnjuki* sp. nov. (from sample P.25) and *A. tsegelnjuki* sp. nov.? (from sample P.30). B, variation of the length of the vesicle (L) with regard to the length of the chamber (l) for *A. tsegelnjuki* sp. nov. (open squares) and *A. tsegelnjuki* sp. nov.? (black squares). C, variation of the length of the vesicle (L) with regard to the diameter of the chamber (D) for *A. tsegelnjuki* sp. nov. (open squares) and *A. tsegelnjuki* sp. nov.? (black squares).

Diagnosis. An *Angochitina* species provided with an ovoid to pear-shaped chamber; neck shorter than the chamber and ending with a flaring membranous collarete; ornamentation of tiny spines densely distributed on the whole vesicle and of a few multirooted spines restricted to the chamber.

Description. This medium-sized new species (L = 163 μ m; D = 75 μ m) is characterized by an ovoid to pear-shaped chamber passing progressively to a fairly short neck flaring toward the aperture. This neck, including

a widened membranous collarete, is shorter than the length of the chamber ($L/l = 1.86$). The flexure is usually poorly marked (Pl. 3, fig. 6a), especially when the vesicle is flattened (Pl. 3, figs 3–4). Tiny spines (length up to $15\text{ }\mu\text{m}$ when complete; diameter over $1\text{ }\mu\text{m}$), usually simple or of lambda type (Pl. 3, fig. 7b), cover the entire vesicle, but fade away on the collarete and on the apex of the chamber (Pl. 3, figs 3–4). They may occur together with a few multirooted and better developed spines (Pl. 3, fig. 6b). This spiny ornamentation is fragile and usually only the proximal part is preserved. The aperture is straight to slightly denticulate (Pl. 3, fig. 3).

Dimensions (Text-fig. 4A–C). Thirty-five specimens in full relief from sample P.25 were measured (values in microns).

	L	l	D	d	dcoll.
Holotype	174	99	73	27	47
Mean	163	87	75	32	48
Range	218–135	109–70	91–57	49–23	67–34

Remarks. *Angochitina crassispina pelosa* Schweineberg, 1987, from the Los Arroyacas Formation (Pridolí of Spain), has a conspicuous flexure and a better developed neck than *Angochitina tsegelnjuki* sp. nov. In addition, the multirooted spines scattered within the ornamentation of the Spanish form are more robust than those of *A. tsegelnjuki* sp. nov. Our new species has also a silhouette different from that of *Angochitina hypenetes* Winchester-Seeto, 1993 from the Lochkovian of Australia.

In Podolia, higher up in the succession, in the lower part of the Chortkov group, sample P.29 yields a very closely related form which we tentatively call *A. tsegelnjuki* sp. nov.? This form differs only from the type material of our new species by its greater dimensions (see mean values below) and by the peculiar design of the proximal ends of its multirooted spines which are more or less parallel to the longitudinal axis of the vesicle (Pl. 4, fig. 10a–b).

Stratigraphical range. *Angochitina tsegelnjuki* sp. nov. ranges from the upper part of the Mitkov Formation to the lower part of the Bogdanovka Formation. These strata are Lochkovian as they yield *E. bohémica* (see discussion above).

Angochitina tsegelnjuki sp. nov.?

Plate 4, figure 10a–b

Material. 276 specimens, both flattened or in full relief, recorded in sample P.29.

Description. This *Angochitina* form has an ovoid chamber provided with a large widened membranous collarete. The length of the chamber is similar to that of the neck. The whole vesicle is covered by tiny multirooted spines (Pl. 4, fig. 10b) which are less developed on the chamber bottom and on the collarete (Pl. 4, fig. 10a). The bases of these spines are more-or-less parallel. However, they are not arranged in true crests.

Dimensions (Text-fig. 4A–C). Based on 20 specimens in full relief from sample P.29 (measurements in microns).

	L	l	D	d	dcoll.
Mean	209	113	84	40	60
Range	244–182	130–99	106–75	52–32	72–52

Remarks. The histogram of the vesicle length (L) clearly shows a bimodal distribution between *A. tsegelnjuki* sp. nov. from sample P.25 and *A. tsegelnjuki* sp. nov.? from sample P.29. This suggests the occurrence of two distinct populations. However, due to the lack of abundant individuals between samples P.25 and P.29, it is difficult to decide if these populations represent the two extremes of an evolutionary trend within a single species, or two separate species. For that reason, we use only a question-mark to distinguish the two forms.

Stratigraphical range. *Angochitina tsegehnjuki* sp. nov.? occurs mainly in sample P. 29 from the lower part of the Bogdanovka Formation, Lochkovian (see stratigraphical discussion above).

Sub family ANCYROCHITININAE Paris, 1981

Genus ANCYROCHITINA Eisenack, 1955

Type species. *Conochitina ancyrea* Eisenack, 1931.

Ancyrochitina sp. nov. A

Plate 2, figure 10a–b

Material. Two specimens from sample P. 19; topmost Tajna Formation.

Description. This small *Ancyrochitina* species is very distinctive because of the occurrence of five or six wide 'crested' processes which are distributed around the margin (Pl. 2, fig. 10a). These 'crested' processes seem to issue from large hollow processes which are open distally and end with a deeply indented membrane simulating a crown of branched straps (Pl. 2, fig. 10b).

This new species is kept in open nomenclature due to insufficient material. However, it seems to have stratigraphical potential as it is already known at a depth of 2040–30 m, in core 12 from well A1–61, Lochkovian of western Libya (Paris unpublished data).

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REASSESSMENT OF EXTINCTION PATTERNS AMONG THE LATE PLEISTOCENE MAMMALS OF SOUTH AMERICA

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ABSTRACT. After the formation of the Isthmus of Panama, about 2.5 Ma, a massive interchange between the previously separated mammalian faunas of South and North America took place. Afterwards, during the Late Pleistocene (Lujanian Land Mammal Age)–Holocene transition (less than 10000 years BP), many of the taxa originally present in South America became extinct. Here, we report results of a statistical assessment of the relative importance of factors potentially associated with extinctions. Several factors (namely trophic niche, origin, and body size) were tested for their association with the probability of extinction, but body mass was the *only* factor found to be significantly correlated with the probability of extinction ($P < 0.0001$). The reduction in deviance with the inclusion of body mass was 55.7 per cent. The fate of 85.6 per cent. of the 120 Late Pleistocene mammalian genera included in the analyses was in accordance with the predictions of a logistic regression model based only on body mass. Trophic niche and origin were also considered, but turned out not to be statistically significant. We propose that the greater resilience against extinction of North American mammalian contingents played no role in the dynamics of the interchange. Also, the analyses demonstrated that marsupials did not go extinct more than placentals. Mammals of North American origin were successful invaders of the South American subcontinent because of their higher speciation rate, and not because of their lower extinction rates.

THIS study constitutes a reassessment of one aspect of the much debated Great American Biotic Interchange (GABI), specifically the hypothesis postulating a competitive displacement of native South American mammal stocks by their colonizing North American counterparts.

After the formation of the Isthmus of Panama, about 2.5 Ma, a massive interchange took place between the previously separated mammalian faunas of South and North America (Webb 1976; Marshall *et al.* 1982). Afterwards, during the Late Pleistocene (Lujanian Land Mammal Age)–Holocene transition (less than 10000 years BP), many of the native South American taxa became extinct (Simpson 1980). These phenomena and their relationships have received wide attention, but the causes of the extinctions associated with the interchange remain controversial (Owen-Smith 1987; Marshall 1988; Webb 1991). Simpson's (1950, 1980) classical hypothesis contends that the main cause of extinction was the superiority of the faunal contingents of North American origin, which would have outfought their South American counterparts in the struggle for life. This hypothesis of 'competitive displacement' has been championed by Webb (1976, 1985). Even though it has been criticized by other researchers (see below), it remains, explicitly or not, the predominant point of view.

By way of example, Gould (1980, following Parker 1977) attributed the comparative misfortune of marsupials in regard to placentals (a subject we will discuss below) not to their intrinsic lack of evolutionary advantages but to their previous evolutionary history in the relative isolation of their South American homeland. Bakker (1986, p. 443) stated that 'North American immigrants devastated the native fauna', and that 'most of the big South American species went extinct, victims of predation and competition from the northerners'. Also, Novacek (1986), in his review of Stehli and Webb (1985), stated that 'the North American components of this exchange brought havoc to much of South America's resident mammal fauna, forcing the extinctions of many lineages'. A more

prudent point of view was held by Marshall (1988), but the notion that the interaction with the North American competition-experts overwhelmed their isolation-accustomed South American counterparts pervaded the paper, in which it was euphemistically said that 'these differences in the histories... signalled the fact that aspects of the interchange would be different on each continent'.

Some authors have questioned the biological bases of the 'competitive displacement' hypothesis, indicating that the ecological equivalence of the alleged North and South American competitors is unclear and that several of the South American endemic stocks began their decline well before the arrival of North American immigrants (Patterson and Pascual 1972; Marshall and Hecht 1978; Benton 1987, 1991; Goin 1989; Ortiz Jaureguizar 1989; Pascual 1989). Unfortunately, discussions of this subject have relied primarily upon either qualitative assessments, lacking the rigour of advanced statistical tests (Stehli and Webb 1985), or analyses of pairs of allegedly equivalent groups, chosen to show a general pattern from such examples (Webb 1976, 1991; but see Marshall and Hecht 1978). We think that specific cases can only be used following the demonstration of the general patterns they mean to illustrate.

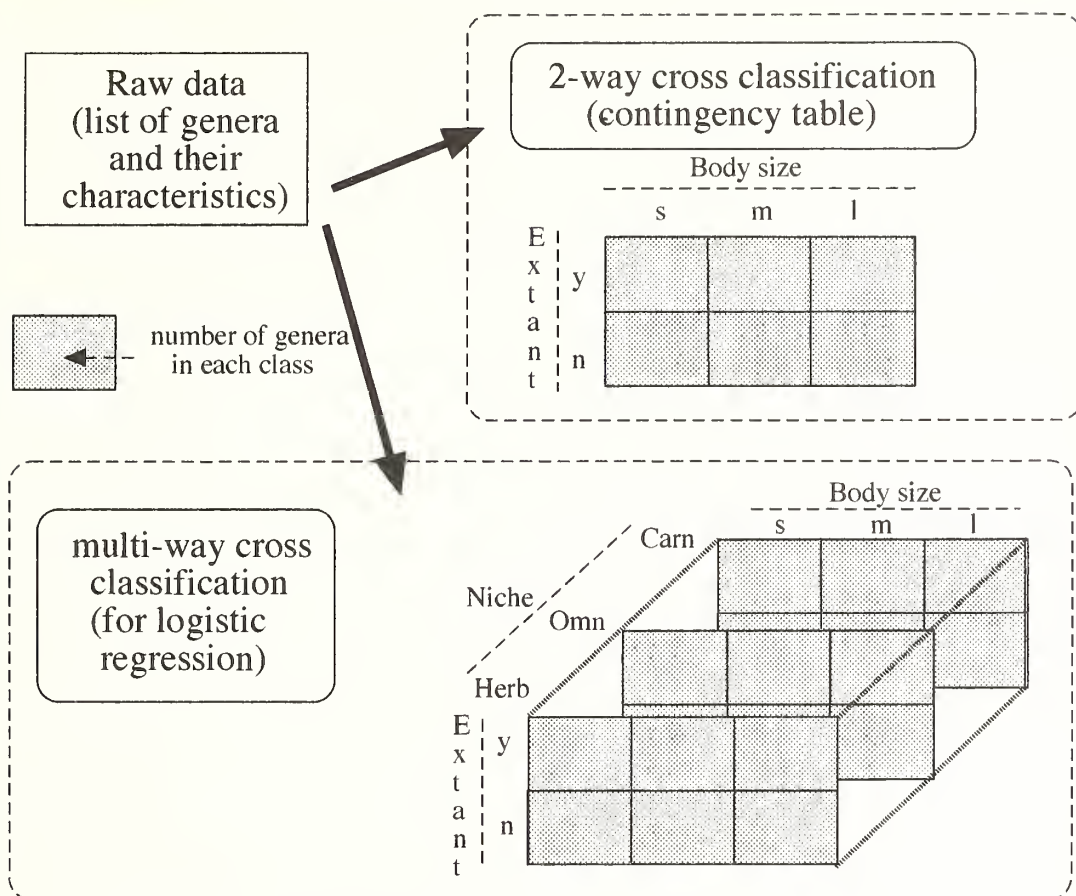
The question to be asked at this point is not really why North American contingents did better than their South American counterparts but whether and, if so, in what sense. The prevailing view taken as a whole, i.e. that North American contingents outcompeted South American ones, is difficult to assess (let alone test statistically). However, we have identified one aspect amenable to statistical testing and have adopted a suitable statistical approach. In particular, we have focused on a specific corollary from Simpson's hypothesis, which predicts an extinction bias with regard to origin among the mammals present in South American following the interchange. One variant of this hypothesis focuses instead on the differences between marsupials and placentals; while the specific reasons are debated, the superiority of placentals over marsupials has been taken almost for granted (but see Parker 1977; Gould 1980).

To test either variant of the classical viewpoint, the body sizes of the genera involved must be taken into account. Indeed, body size is widely regarded as a major factor in determining a species' susceptibility to extinction (Flessa *et al.* 1986; Pimm 1991), both in general and especially in the case under study. We presumed that neither variant would stand a statistical test after body size and other relevant factors different from origin or 'marsupialness' had been included.

For testing these hypotheses, we adopt here a global, quantitative approach of the whole mammal fauna involved. Our analysis compares extinction rates of North and South American mammal contingents, themselves heterogeneous from a phylogenetic standpoint. The conceptual framework was developed for the macroevolutionary processes of competition among species and monophyletic taxa, but it can be readily utilized in our assessment of the relative success of these contingents. We focus here on death bias (Gould 1982) as a potential pattern favouring certain taxa at the expense of others.

MATERIAL AND METHODS

Factors and data set. We have addressed the relative predictive value and statistical significance of various factors, chosen for their presumed correlation with the probability of extinction. We took 120 of the genera listed by Marshall *et al.* (1984) for the Late Pleistocene (Lujanian Land Mammal Age) of South America and classified them according to the following characteristics (Appendix 1): 1. Their origin, i.e. the South or North American source of the family before the beginning of the interchange in the Late Pliocene (*c.* 2.5 Ma). Sigmodontine rodents were classified as North American in origin. Although some scholars contend that their invasion of South America might have preceded the formation of the Isthmus of Panama (Hershkovitz 1966; Reig 1981), their classification here as of North American origin would, in any case, favour Simpson's point of view. 2. Their trophic niche, initially including six, later grouped into three, categories (carnivores, omnivores and herbivores). This reduction undoubtedly made the trophic classification relatively coarse. A more refined subdivision, as used by Patterson (1984), however, cannot yet be achieved for exclusively fossil South American mammals, because their palaeobiology has not received enough attention to permit sound hypotheses about their inferred habits.



TEXT-FIG. 1. Diagram representing the processing of data for analysis. To ask whether extinction is correlated with body size, for example, one needs a two-way cross classification summarizing how many genera of each size class are living or extinct. A χ^2 -test may be carried out using those data. An analysis attempting to assess the association of extinction with several other factors requires a multi-way classification, of which the 3-way table in the figure (bottom) is an example. s = small; m = medium; l = large; y = yes; n = no. See Appendix for other abbreviations.

3. Their mass, comprising three categories (less than 1 kg, between 1 and 100 kg, and more than 100 kg). Something must be said here about introduction of a possible size-related taphonomic bias (Damuth 1982). Although some groups of small mammals, especially the forest-dwelling primates, are not represented in the Lujanian sample, our analysis is not critically affected, because we are comparing genera living in the Lujanian, regardless of whether or not they became extinct in the Recent. Only a very different pattern of extinction among underrepresented groups could significantly change our conclusions.

A separate analysis excluded origin and replaced it by 'marsupialness,' a variable classifying taxa as either marsupials or placentals. This allowed us to test for any relevant differences between marsupials and placentals with respect to extinction.

The classification criteria outlined above are generally conservative. We preferred our data to be coarse and reliable, rather than finer and doubtful.

Statistical analysis. The first set of analyses was carried out on contingency tables cross-classifying each of the factors described above with the extinct-extant status of the genera. For each contingency table, χ^2 -tests were utilized to assess whether extinctions were independent from the factors in question. Notice that these tests take factors one at a time.

Additionally, the data were analysed by means of a stepwise, maximum likelihood logistic regression, an analogue of multiple regression suitable for dealing with qualitative response variables (McCullagh 1980; McCullagh and Nelder 1989). This procedure allows the sequential or simultaneous inclusion of factors into the model to assess their statistical significance and predictive value. These analyses were carried out by fitting logistic regression models using SAS-PC (SAS Institute 1992). The reduction in deviance after the inclusion of each factor estimates its relative importance. The models were examined for their goodness of fit.

A diagrammatic representation of our statistical approaches is presented in Text-figure 1. All analyses share the fact that they are based on cross-classification of several factors.

RESULTS

The χ^2 -tests of contingency tables suggested that, taken one at a time, all factors except origin were significantly correlated with the probability of extinction (Table 1). Unsurprisingly, body size shows the most dramatic association with extinctions, but niche and marsupialness are also significant. The latter is interesting in that marsupials appear less, not more prone to extinction than placentals.

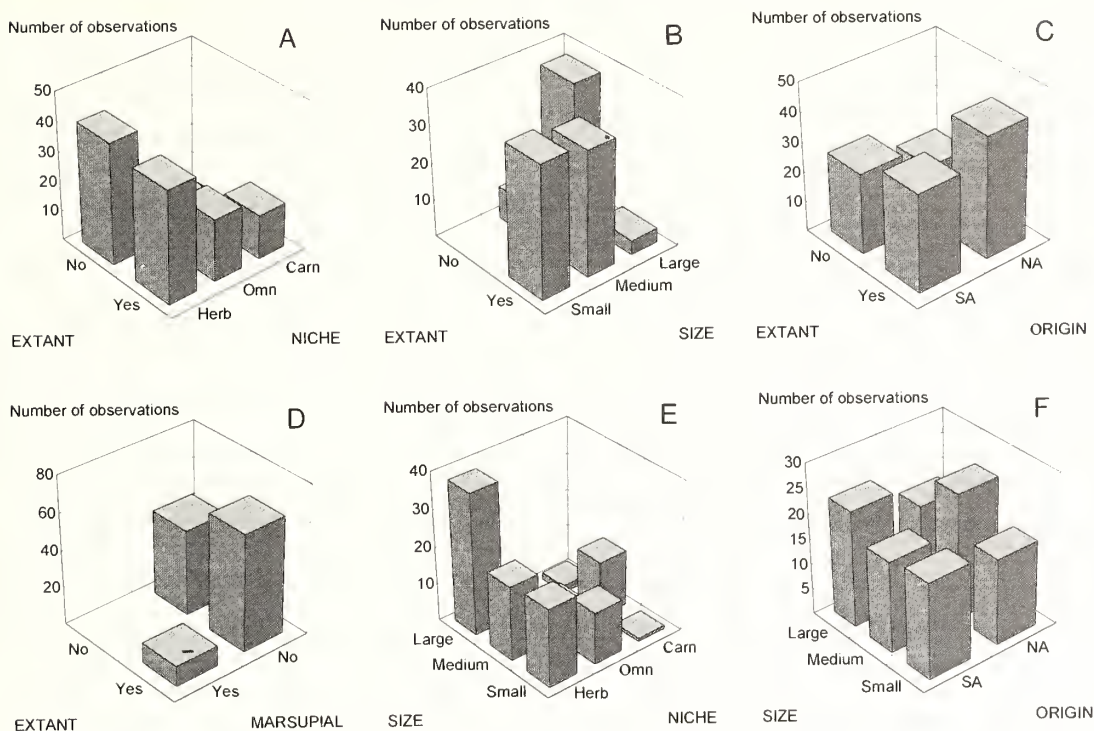
TABLE 1. Summary statistics of contingency tables testing the independence of extinction with regard to several factors.

Factor	Degrees of freedom	χ^2	P
Body mass	2	74.625	0.001
Niche	2	18.271	0.001
Origin	1	2.256	0.133
Marsupial/placental	1	7.528	0.006

The data on which the analyses are based are depicted in Text-figure 2. Although, as just indicated, not all associations are significant, Text-figure 2 shows the following trends: (1) herbivores were more prone to extinction than omnivores or carnivores; (2) so were large animals

TABLE 2. Results of a stepwise logistic regression using origin, niche and body mass as factors to predict the probability of extinction among Late Pleistocene South American mammals.

Factor	Included in the model?	P
<i>A. Standard data set</i>		
Intercept	Yes	0.0001
Body mass	Yes	0.0001
Niche	No	0.1003
Origin	No	0.1318
<i>B. Marsupial/placental factor instead of origin</i>		
Intercept	Yes	0.0001
Body mass	Yes	0.0001
Niche	No	0.1003
Marsupial/placental	No	0.4432



TEXT-FIG. 2. Frequency histograms of several combinations of the variables examined in this study. On the left hand side niche (A), size (B), and origin (C) are examined in relation to the current status of the genera (extant or extinct). The status of marsupials and placentals are similarly examined in D. Finally, it is shown that niche and origin are correlated with size (E-F), i.e. that the categories in those factors are biased with respect to body mass. Thus, size, niche and origin are not independent from each other. See Appendix for abbreviations.

compared with smaller ones; and (3) South American residents compared with North American immigrants; as well as (4) placentals relative to marsupials.

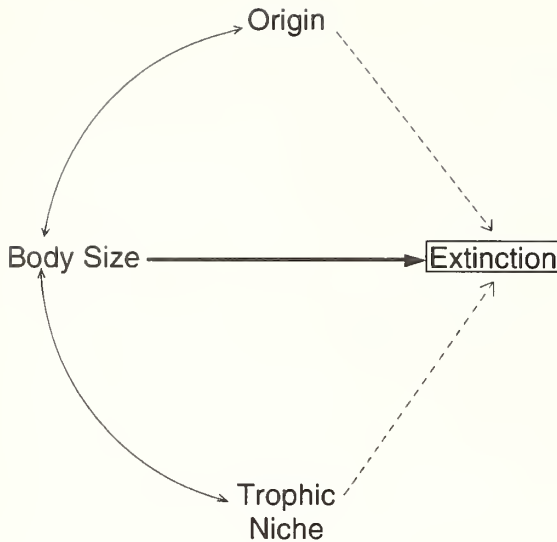
In contrast with the results of two-way contingency tables, logistic regression analyses (Table 2) indicated that only body mass was statistically significant, and very highly so ($P < 0.0001$). The inclusion of body mass alone reduced the deviance by 55.7 per cent. The additional inclusion of trophic niche and origin was not warranted (Table 2).

Again, the data depicted in Text-figure 2 may help understand the contrast between logistic regression, that singles out body size as the only significant factor associated with extinction, and two-way contingency tables, in which niche is significant as well. Size and niche are correlated, primarily because large animals tend to be herbivores, and both factors are significant in relation to extinction taken one at a time. Once size is included in a logistic regression, the significance of niche disappears, most probably because it indirectly reflects the importance of body size.

Replacing the factor origin with the factor 'marsupialness' did not change the situation; the hypothesis that the condition of being marsupial was not relevant to the proneness to extinction could not be rejected ($P < 0.4432$).

DISCUSSION AND CONCLUSIONS

It can be clearly concluded that, among the factors discussed above, body size is, as expected, overwhelming in its predictive value. In agreement with other cases of large-scale extinctions, larger South American mammals tended to become extinct significantly more often than smaller ones



TEXT-FIG. 3. Diagrammatic summary of our interpretation of the data. Only one factor (body size) accounts for the likelihood of extinction among late Pleistocene South American mammals. However, because niche and origin are correlated with body size, they may also show correlation with extinction. Such correlation disappears in logistic regressions that consider those factors simultaneously.

(Martin and Klein 1984; Benton 1990; Raup 1993). Thus, and as in other extinction events, the higher specialization that large size implies led to a differential extinction of large mammals.

This result is not surprising in itself, but suggests that considering other factors in the absence of body size data would be inappropriate. Thus, several factors showed statistical significance in the contingency tables, but such significance disappeared when those factors were considered simultaneously in a stepwise logistic regression. This indicates, firstly, that those factors are not independent of each other. As an obvious example, body mass and trophic niche are not uncorrelated in nature. Secondly, and more importantly, the statistically significant results of contingency tables for many of the factors are all heavily influenced by the hidden but pervasive influence of body mass in all analyses. Logistic regression permits identification of body mass as the only factor significantly correlated with extinction in the end of the Lujanian.

Text-figure 3 summarizes our hypothesis about the relationships between niche, origin, body mass and extinction. We propose that body mass is the only factor directly correlated with extinction because of its overriding ecological and demographic significance. Since niche and origin are correlated with body size (i.e. are biased with respect to body size), they may show indirect correlation with extinction. The statistical significance of such correlation, if present, as in the case of niche, should and does disappear when this factor is considered simultaneously with body size.

Statistical significance and causation are different matters, but it can be stated that the pattern revealed by the analyses is consistent with previously proposed processes that would primarily affect large animals, e.g. that large mammals were more vulnerable to the human *blitzkrieg* (Martin and Klein 1984), or that the large mammals were less capable of facing adverse climate changes during the Pleistocene-Holocene transition (see Marshall and Cifelli 1990 for review).

Origin, a much discussed factor presumably correlated with extinction, was not significant taken in isolation or in the context of logistic regressions (Tables 1 and 2). Mammals of South American pedigree were no more prone to die out than their North American counterparts. Contrary to theoretical expectations (Patterson 1984), trophic niche was not a significant factor in these analyses. This may be due to the overriding effect of body mass or to the inevitably coarse subdivision of niches in our data set.

The hypothesis proposing the evolutionary inferiority of marsupials was refuted, at least in connection with this particular extinction phenomenon.

Our analyses show that Simpson was not correct in his statement that mammals of North American origin were less prone to extinction than those of South American origin at the

Pleistocene–Holocene boundary. However, the North American contingent did show a superiority in having higher diversification patterns after the interchange, as suggested by some authors (Marshall *et al.* 1992).

In fact, using Gould's (1982) terminology of evolution above the species level, it can be stated that the species belonging to the North American invaders were superior to the South American ones due to a birth bias, but not to a death bias in their favour. Indeed, Marshall *et al.* (1982), while establishing a higher figure of extinction rates for natives (0.5 genera per genus per million years, from Huayquerian to Recent) in comparison with immigrants (0.3 genera per genus per million years, for the same period), expressed the possibility that this could have been explained by multiple immigrations rather than by differences in the actual extinction rates. Furthermore, Cione and Tonni (1995) refined the stratigraphy of southern South America, and claimed that the arrival of mammals into that region was not as sudden as previously stated.

One possible objection to all of our analyses is that we arbitrarily emphasized the latest extinction event of what was in fact a protracted and presumably complex process of faunal dynamics. Granted, ours is a limited focus, but this results from several biological and statistical considerations. Two points must be mentioned in this respect:

1. Earlier extinctions can be regarded as background ones, and only the one considered here is a proper mass extinction. As a matter of fact, 22 per cent. of the genera present in the Early Pleistocene (Marplatian Land Mammal Age; Cione and Tonni 1995) are not found in the Ensenadan, the following Land Mammal Age, and 7 per cent. of the Ensenadan genera are not found in the Lujanian. The percentage of the extinct Lujanian genera is 40 per cent., which qualifies for a mass extinction of intermediate level according to the criterion proposed by Sepkoski (1986) at a global scale, and is actually higher than the percentage of genera which became extinct in the Cretaceous–Tertiary boundary event. The percentages of extinction between preceding strata, in contrast, are well within values given by Raup and Sepkoski (1986) for background or minor extinctions.

2. The fortunate fact that post-Lujanian extinctions were most significant after the Great American Interchange allowed us to approach the requirements of the statistical methodologies employed in our assessment. No other comparison of strata comes closer to meeting the requirement of an unequivocal classification of all taxa to be employed with respect to the factors to be utilized. Taxonomic uncertainties are no less of a factor in our case, but we can assert that a taxon became extinct or survived the Lujanian with much greater confidence.

In conclusion, we investigated the most significant period of extinctions following the Great American Interchange, for which the quantity and quality of data happen to be the best. Earlier phases of the interchange simply fail to comply with these characteristics.

It could be argued that the displacement of the least fit South American taxa took place at an earlier phase, but then the fitter North American stocks remaining should still have been able to outcompete their remaining native competitors.

We also carried out analyses specifically directed at alternative ways of classifying some of the taxa in our data. For instance, one of us (Fariña in press) claimed, on palaeoecological grounds, that ground sloths could have been opportunistic flesh eaters. The analysis was run with the due change in the data, i.e. ground sloths were taken as omnivorous, but the results were very similar. The niche was again non-significant as a factor explaining extinction, and, more generally, results did not change substantially for the factors considered. Another potential source of bias in the results was the fact that sigmodontine cricetids were considered as having a North American origin, but, again, the changes in the figures yielded by the analysis classifying them as South American were only minor. Finally, we conducted a separate logistic regression on the basis of the genera listed by Tonni *et al.* (1992) for the Pampean region, by far the best documented Late Pleistocene fauna of South America, and, once more, body mass turned out to be the only significant factor associated with extinction. In sum, the alternatives tested so far do not change our fundamental results.

The analytical power of logistic regression and related statistical tools is well illustrated by our analyses. Such tools will be useful in future studies of the causes of extinction, such as the differences

in extinction rates between mammals of open country and forested habitats (Vrba 1992). Additionally, progress on the issue of extinction patterns will require further refinement of the categories utilized in the data analysis.

The invasion by North American mammal contingents had a dramatic impact upon the faunal composition of South America. Differential extinction of both stocks, however, cannot account for such an effect, the causes of which must be sought elsewhere (for reviews of various proposals, see Martin and Klein 1984; Marshall and Cifelli 1990; Webb 1991).

On the other hand, North American invaders were very successful in doing precisely that, i.e. invading. Pimm (1991) analysed the difficulties faced by any species invading a new habitat. Many species belonging to the North America mammal fauna succeeded in this task when a land bridge was available, and even before. Moreover, once established, they speciated much more than the endemics, and hence their number grew exponentially (Webb and Marshall 1982).

Unfortunately, other factors involved in faunal dynamics, such as differential speciation, cannot be tested as easily, since logistic regression requires a reliable and complete cross-classification of all taxa for all factors.

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APPENDIX

List of genera considered in the analysis. Their origin has been classified as either South or North American, their trophic niche as herbivore, omnivore or carnivore, and their size as small, medium or large, according to the criteria discussed in the text. * = marsupials; NA = North American; SA = South American; Carn = carnivorous; Herb = herbivorous; Omn = omnivorous.

Genus	Extant	Origin	Niche	Size
1 <i>Caluromys</i> *	Yes	SA	Omn	Small
2 <i>Chironectes</i> *	Yes	SA	Omn	Small
3 <i>Didelphis</i> *	Yes	SA	Omn	Medium
4 <i>Lestodelphys</i> *	Yes	SA	Omn	Small
5 <i>Lutreolina</i> *	Yes	SA	Omn	Small
6 <i>Marmosa</i> *	Yes	SA	Omn	Small
7 <i>Micoureus</i> *	Yes	SA	Omn	Small
8 <i>Metachirus</i> *	Yes	SA	Omn	Medium
9 <i>Monodelphis</i> *	Yes	SA	Omn	Small
10 <i>Philander</i> *	Yes	SA	Omn	Small
11 <i>Thylamys</i> *	Yes	SA	Omn	Small
12 <i>Cryptotis</i>	Yes	NA	Omn	Small
13 <i>Cabassous</i>	Yes	SA	Omn	Medium
14 <i>Chaetophractus</i>	Yes	SA	Omn	Medium
15 <i>Chlamyphorus</i>	Yes	SA	Omn	Small
16 <i>Dasyus</i>	Yes	SA	Omn	Medium
17 <i>Euphractus</i>	Yes	SA	Omn	Medium
18 <i>Eutatus</i>	No	SA	Herb	Medium
19 <i>Pampatherium</i>	No	SA	Herb	Large
20 <i>Propaopus</i>	No	SA	Omn	Medium
21 <i>Tolypeutes</i>	Yes	SA	Herb	Medium
22 <i>Zaedyus</i>	Yes	SA	Omn	Medium
23 <i>Chlamydotherrum</i>	No	SA	Herb	Large
24 <i>Doedicurus</i>	No	SA	Herb	Large
25 <i>Glyptodon</i>	No	SA	Herb	Large
26 <i>Hoplophorus</i>	No	SA	Herb	Large
27 <i>Neothoracophorus</i>	No	SA	Herb	Large
28 <i>Panochthus</i>	No	SA	Herb	Large
29 <i>Plaxhaplous</i>	No	SA	Herb	Large
30 <i>Sclerocalypus</i>	No	SA	Herb	Large
31 <i>Nothropus</i>	No	SA	Herb	Medium
32 <i>Nothrotherium</i>	No	SA	Herb	Large
33 <i>Ocnopus</i>	No	SA	Herb	Large
34 <i>Valgipes</i>	No	SA	Herb	Medium
35 <i>Eremotherium</i>	No	SA	Herb	Large
36 <i>Megatherium</i>	No	SA	Herb	Large
37 <i>Glossotherium</i>	No	SA	Herb	Large
38 <i>Lestodon</i>	No	SA	Herb	Large
39 <i>Mylodon</i>	No	SA	Herb	Large
40 <i>Scelidodon</i>	No	SA	Herb	Large
41 <i>Scelidotherium</i>	No	SA	Herb	Large
42 <i>Sylvilagus</i>	Yes	NA	Herb	Medium
43 <i>Akodon</i>	Yes	NA	Herb	Small
44 <i>Andinomys</i>	Yes	NA	Herb	Small
45 <i>Auliscomys</i>	Yes	NA	Herb	Small
46 <i>Bolomys</i>	Yes	NA	Omn	Small
47 <i>Calomys</i>	Yes	NA	Herb	Small

Genus	Extant	Origin	Niche	Size
48 <i>Eligmodontia</i>	Yes	NA	Herb	Small
49 <i>Euneomys</i>	Yes	NA	Herb	Small
50 <i>Graomys</i>	Yes	NA	Herb	Small
51 <i>Holochilus</i>	Yes	NA	Herb	Small
52 <i>Kunsia</i>	Yes	NA	Herb	Small
53 <i>Nectomys</i>	Yes	NA	Herb	Small
54 <i>Oxymycterus</i>	Yes	NA	Omn	Small
55 <i>Phyllotis</i>	Yes	NA	Herb	Small
56 <i>Reithrodon</i>	Yes	NA	Herb	Small
57 <i>Scapteromys</i>	Yes	NA	Omn	Small
58 <i>Ctenomys</i>	Yes	SA	Herb	Small
59 <i>Abrocoma</i>	Yes	SA	Herb	Small
60 <i>Carterodon</i>	Yes	SA	Herb	Small
61 <i>Euryzygomatomys</i>	Yes	SA	Herb	Small
62 <i>Proechimys</i>	Yes	SA	Herb	Small
63 <i>Thrichomys</i>	Yes	SA	Herb	Small
64 <i>Myocastor</i>	Yes	SA	Herb	Medium
65 <i>Lagostomus</i>	Yes	SA	Herb	Medium
66 <i>Lagidium</i>	Yes	SA	Herb	Medium
67 <i>Coendou</i>	Yes	SA	Herb	Medium
68 <i>Cavia</i>	Yes	SA	Herb	Small
69 <i>Dolichotis</i>	Yes	SA	Herb	Medium
70 <i>Galea</i>	Yes	SA	Herb	Small
71 <i>Microcavia</i>	Yes	SA	Herb	Small
72 <i>Hydrochoerus</i>	Yes	SA	Herb	Medium
73 <i>Nechoerus</i>	No	SA	Herb	Large
74 <i>Canis</i>	Yes	NA	Carn	Medium
75 <i>Cerdocyon</i>	Yes	NA	Carn	Medium
76 <i>Chrysocyon</i>	Yes	NA	Carn	Medium
77 <i>Dusicyon</i>	Yes	NA	Carn	Medium
78 <i>Lycalopex</i>	Yes	NA	Carn	Medium
79 <i>Protocyon</i>	No	NA	Carn	Medium
80 <i>Speothos</i>	Yes	NA	Carn	Medium
81 <i>Theriodictis</i>	No	NA	Carn	Medium
82 <i>Arctodus</i>	No	NA	Omn	Large
83 <i>Nasua</i>	Yes	NA	Carn	Medium
84 <i>Conepatus</i>	Yes	NA	Carn	Medium
85 <i>Galera</i>	Yes	NA	Carn	Medium
86 <i>Galictis</i>	Yes	NA	Carn	Medium
87 <i>Lyncodon</i>	Yes	NA	Carn	Medium
88 <i>Lutra</i>	Yes	NA	Carn	Medium
89 <i>Mustela</i>	Yes	NA	Carn	Small
90 <i>Felis</i>	Yes	NA	Carn	Medium
91 <i>Leo</i>	Yes	NA	Carn	Large
92 <i>Smilodon</i>	No	NA	Carn	Large
93 <i>Macrauchenia</i>	No	SA	Herb	Large
94 <i>Windhausenina</i>	No	SA	Herb	Large
95 <i>Mixotoxodon</i>	No	SA	Herb	Large
96 <i>Toxodon</i>	No	SA	Herb	Large
97 <i>Cuvieronius</i>	No	NA	Herb	Large
98 <i>Haplomastodon</i>	No	NA	Herb	Large
99 <i>Natiomastodon</i>	No	NA	Herb	Large

Genus	Extant	Origin	Niche	Size
100 <i>Stegomastodon</i>	No	NA	Herb	Large
101 <i>Equus</i>	No	NA	Herb	Large
102 <i>Hippidion</i>	No	NA	Herb	Large
103 <i>Onohippidion</i>	No	NA	Herb	Large
104 <i>Tapirus</i>	Yes	NA	Herb	Large
105 <i>Brasiliochoerus</i>	No	NA	Herb	Medium
106 <i>Catagonus</i>	Yes	NA	Herb	Medium
107 <i>Tayassu</i>	Yes	NA	Herb	Medium
108 <i>Platygonus</i>	No	NA	Herb	Large
109 <i>Eulamaops</i>	No	NA	Herb	Large
110 <i>Lama</i>	Yes	NA	Herb	Large
111 <i>Palaeolama</i>	No	NA	Herb	Large
112 <i>Agalmaceros</i>	No	NA	Herb	Large
113 <i>Blastocerus</i>	Yes	NA	Herb	Large
114 <i>Hippocamelus</i>	Yes	NA	Herb	Medium
115 <i>Mazama</i>	Yes	NA	Herb	Medium
116 <i>Morenelaphus</i>	No	NA	Herb	Medium
117 <i>Odocoileus</i>	Yes	NA	Herb	Medium
118 <i>Ozotoceros</i>	Yes	NA	Herb	Medium
119 <i>Paraceros</i>	No	NA	Herb	Medium
120 <i>Antifer</i>	No	NA	Herb	Large

A CLADISTIC ANALYSIS OF THE HORSES OF THE TRIBE EQUINI

by JOSÉ L. PRADO and MARÍA T. ALBERDI

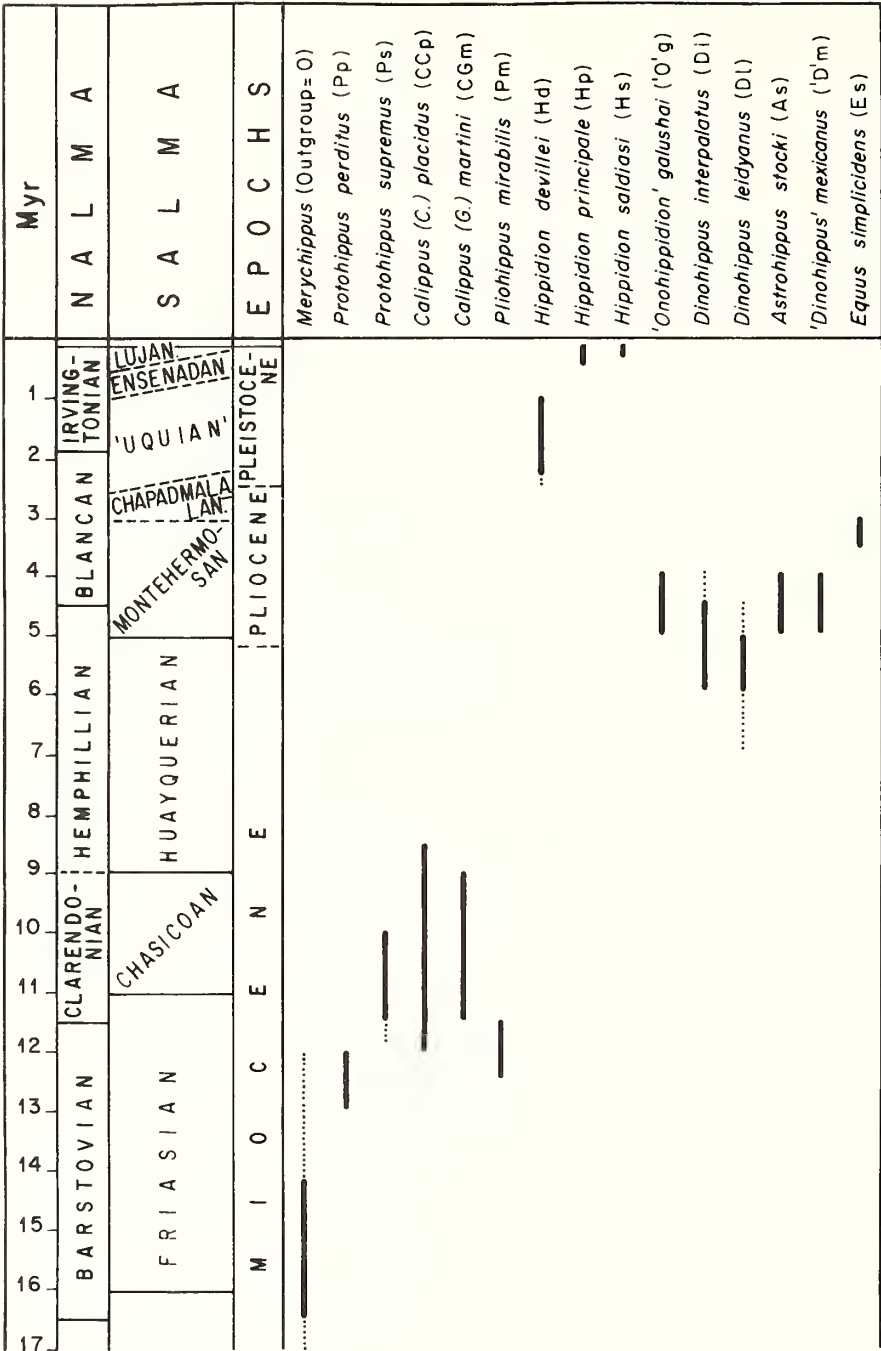
ABSTRACT. The Equini tribe with seven genera forms a monophyletic group defined by one synapomorphy: protocone connected to the protoloph. Fourteen species are considered as the terminal taxa: *Protohippus* (two species), *Calippus* (two), *Pliohippus* (one), *Hippidion* (three), *Dinohippus* (three), *Astrohippus* (one) and *Equus* (two). A cladistic analysis was performed using 20 characters from cranial morphology, upper and lower teeth, and appendicular skeletons. Polarity of characters was based on outgroup criterion using the Hippotheriini tribe. For some characters, apomorphic states were identified using *Merychippus*, which was the sister group of both tribes. One parsimonious cladogram of 31 steps and a consistency index of 0.77 was produced, from which a classification of the tribe Equini was constructed. We recognize two subtribes: Protohippina (*Protohippus* and *Calippus*) and Pliohippina subtrib. nov. (*Pliohippus*, *Hippidion*, *Dinohippus*, *Astrohippus* and *Equus*). *Pliohippus* was the sister group to the rest of the subtribe. The species of *Hippidion* form a monophyletic group and there is no evidence of a relationship between '*Onohippidium*' *galushai*, from North America, and the *Hippidion* group, from South America. *Astrohippus stocki* was the sister species of the *Equus*-group, which includes '*Dinohippus*' *mexicanus*. The analysis shows that characters mostly from the cranial morphology and upper teeth characterize the suprageneric taxa. High congruence between the stratigraphical record and the phylogenetic hypothesis is observed.

THE subfamily Equinae Gray is clearly recognizable as a monophyletic group on the basis of at least five major shared-derived character states of the cheek teeth: (1) cement formed on deciduous and permanent cheek teeth; (2) presence of the pli caballin on premolars and molars; (3) presence of the pli linguaflexid; (4) moderately deep ectoflexid on p2; (5) unworn M1-M2 crown heights greater than 23–28 mm (Hulbert 1988a; Hulbert and MacFadden 1991; MacFadden 1992). This clade represents the major adaptive radiation of hypsodont horses and includes Equini and Hippotheriini (*sensu* Prothero and Schoch 1989, p. 532; = Hipparionini Quinn, 1955).

The Equini tribe comprises eight genera, one widespread throughout the world (*Equus*), six endemic to North America: *Protohippus*, *Calippus*, *Pliohippus*, *Dinohippus*, '*Onohippidium*' and *Astrohippus* (Evander 1989; Hulbert 1989; Prothero and Schoch 1989) and one endemic to South America: *Hippidion* (Alberdi 1987; Alberdi and Prado 1993). The Equini lineage is well-known from the middle Miocene until the upper Pliocene in North America (Text-fig. 1). In South America, the first record of this lineage comes from the upper Pliocene–lower Pleistocene (Marshall *et al.* 1984; Alberdi and Prado 1993). The lineage became extinct during the late Pleistocene (Alberdi and Prado 1993; Martin and Klein 1984; Prado and Alberdi 1994; Politis *et al.* 1995).

Equini is a monophyletic group of genera distinguished from the tribe Hippotheriini (Prothero and Schoch 1989) by at least one apomorphic character state: protocone connected to the protoloph (Hulbert 1988a; Hulbert and MacFadden 1991; MacFadden 1992).

Different phylogenies of equids have been proposed. Some authors (Stirton 1940; Lance 1950; Simpson 1951; Quinn 1955) considered, based on phylogenetic systematics, '*Merychippus*' (*Protohippus*) as an ancestor of *Calippus* and *Pliohippus* and *Pliohippus* to be the ancestor of all *Hippidion*, *Astrohippus* and *Equus* species. On the other hand, Hulbert (1989) and MacFadden (1992) suggested, based on cladistics analysis, *Merychippus* as a sister group of Equini and Hippotheriini tribes (hipparionines and protohippines). *Protohippus* and *Calippus* form a



TEXT-FIG. 1. Chronological distribution of Equini species. Myr = million years; NALMA = North America Land Mammal Ages; SALMA = South America Land Mammal Ages. The stratigraphical framework was taken from Marshall *et al.* (1983, 1984), Tedford *et al.* (1987) and Alberdi *et al.* (1995).

monophyletic group and are set apart from the other genera: *Astrohippus*, *Hippidion*, '*Ouohippidium*', *Dinohippus*, *Equus* and *Pliohippus*.

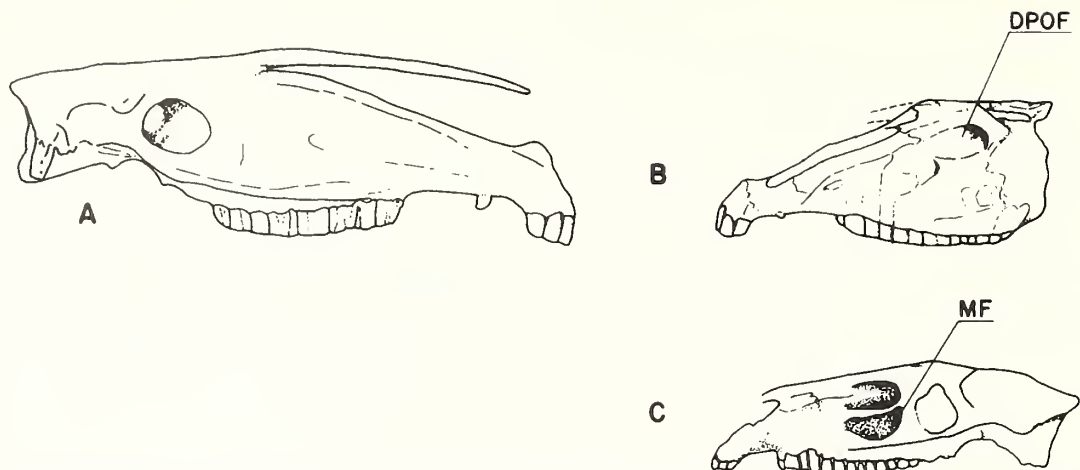
The phylogenetic relationships within the tribe Equini are a matter for debate (e.g. Matthew 1926; Stirton 1940; Quinn 1955; Evander 1989; Hulbert 1989; Prothero and Schoch 1989). This paper comprises a cladistic analysis for this tribe, with special attention to the relation of South American horses, based on data obtained from the cranial and appendicular skeleton morphology. In addition, we examined its congruence with the fossil record.

MATERIAL AND METHODS

We examined 14 species of Equini (Text-fig. 1). Since many species of fossil Equini are very poorly known, we decided to include only the best-known species of each recognized genus (as defined by Evander 1989 and Prothero and Schoch 1989). Specimens of *Protohippus perditus* (FAM 126623, 125626, 60351, and 126759; from Devils Gulch Member, Nebraska, upper Barstovian), *Protohippus supremus* (FAM 12631, 125258 and 111728, from Mac Adams Quarry, Texas, lower Clarendonian), *Pliohippus mirabilis* after Evander (1989), MacFadden (1992), among others (FAM 60810 (skull, mandible and complete skeleton), from Devils Gulch Member, Nebraska, upper Barstovian), *Dinohippus interpolatus* (FAM 87201 and 18972, from Edson Quarry, Kansas, upper Hemphillian), *Dinohippus leidyani* (FAM 116191, 116194, from Guymon quarries, Texas, upper Hemphillian), *Astrohippus stocki* (FAM 74290, 74291 and 74283, from Ogallala Formation, Texas, upper Hemphillian and from Yepómera, Mexico, uppermost Hemphillian in Lance 1950), '*Ouohippidium*' *galushai* (FAM 116136, 31938, 11872, Wikieup Fauna, Arizona, upper Hemphillian, and MacFadden and Skinner 1979) and *Equus simplicidens* (FAM 32550, 32551, 32553, 32535 and 20077, from Hagerman Horse Quarry, Idaho and Crosby Co., Texas, middle Blancan) came from the Frick Collection of the American Museum of Natural History. Data for *Calippus* (*Calippus*) *placidus* and *Calippus* (*Granulohippus*) *martini* were taken from Hulbert (1988a), '*Dinohippus*' *mexicanus* from Lance (1950) and *Hippidion* species from Alberdi and Prado (1993). The review of late Oligocene to early Pliocene mammalian biochronology by Tedford *et al.* 1987 and the recent review of Plio-Pleistocene biochronology from Argentina by Alberdi *et al.* 1995 provided a chronological framework for the analysis.

Character polarity was determined by outgroup comparison methods (Eldredge and Cracraft 1980; Watrous and Wheeler 1981; Humphries and Funk 1984; Maddison *et al.* 1984), collectively using the other tribe (Hippotheriini) of the subfamily Equinae as the outgroup. For some characters, apomorphic states were identified using *Merychippus* (*sensu* Evander 1989; Hulbert 1989; Hulbert and MacFadden 1991), which was the sister group of both tribes. The '*Merychippus*-group' has traditionally been a large polyphyletic assemblage with many species. Recent studies have separated the merychippine grade into a monophyletic clade (MacFadden 1992). The Hippotheriini data were taken from Simpson (1951), Gromova (1952), Forsten (1968), Alberdi (1974) and Watabe (1992).

In current cladistic analysis, missing entries in data matrices represent information that is unknown. This is the case for *Hippidion saldiasi* and '*Dinohippus*' *mexicanus* which are known only from a few remains. The selection of characters is based on a critical review of specimens and the previous literature about cladistic analyses on horses (Bennett 1980; Hulbert 1988a, 1988b; Evander 1989; Hulbert 1989; Hulbert and MacFadden 1991; MacFadden 1992; Watabe 1992). In order to get one parsimony tree we used, where possible, the characters which present the fewest missing data. Consequently, our data matrix has more cranial characters than appendicular skeleton ones. Twenty characters were used: five from the cranial morphology (characters 1–5), six from the upper teeth (characters 6–11), four from the lower teeth (characters 12–15), three from the mandible (characters 16–18), and two from the appendicular skeleton (characters 19–20).



TEXT-FIG. 2. Skull characteristics. A, *Hippidion principale* with nasal notch posterior to M1 (character 1) and long muzzle (character 4); B, '*Onohippidion*' *galushai*; C, *Astrohippus stocki*. DPOF = dorsal preorbital fossa; MF = malar fossa.

Character definition and codification

1. Depth of nasal notch (Text-fig. 2A). Some living mammals, such as tapirs, have retracted nasal bones, which have an adaptation to the presence of a proboscis. This feature, however, is rare in fossil horses, although some *Hipparion* from Eurasia apparently possessed a tapir-like proboscis (Studer 1911; Sefve 1927).

Outgroup comparison. All *Merychippus* species and the primitive group of Hippotheriini (morphotype 1 *sensu* Alberdi 1989) have a nasal notch level with, or anterior to P2 (Hulbert 1988b, 1989; Hulbert and MacFadden 1991; Watabe 1992), which is regarded as primitive.

States. 0 = anterior to P2; 1 = between P2-M1; 2 = posterior to M1.

2. Malar fossa (Text-fig. 2C). The malar fossa of Hulbert (1988b) is the same as the facial fossa of Gregory (1920) and the infracranial fossa of Gromova (1952).

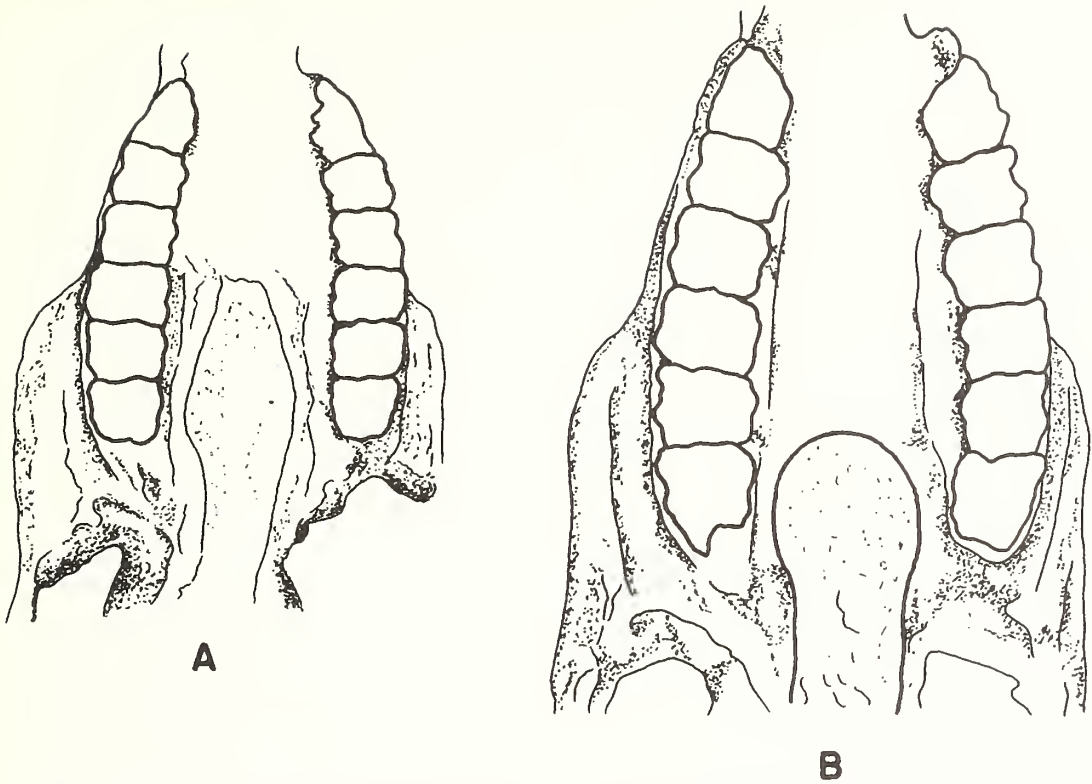
Outgroup comparison. All Hippotheriini species have an absent or shallow malar fossa.

States. 0 = absent or shallow; 1 = present.

3. Dorsal preorbital fossa (DPOF; Text-fig. 2B). This fossa is the same as the lacrimal fossa of Gregory (1920), the supracranial fossa of Gromova (1952), the preorbital fossa of Pirlot (1953) and the nasomaxillary fossa of Skinner and MacFadden (1977). Many authors use the morphology of the DPOF as a taxonomic character in fossil horses. We believe, however, that this is an unstable character (Forsten 1983; Eisenmann *et al.* 1987; Alberdi 1989). According to Gromova (1952) its morphology varies among the ontogenetic states. We used only the presence/absence of this feature but did not consider the morphology.

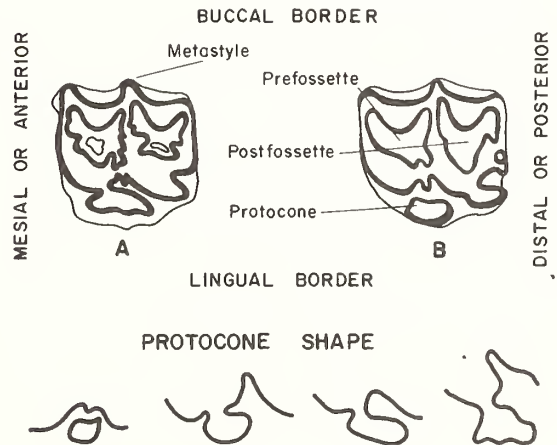
Outgroup comparison. The most derived Hippotheriini species (morphotype 6 *sensu* Alberdi 1989) lost the DPOF (Hulbert 1988b; Watabe 1992). A very well-developed DPOF is regarded as primitive.

States. 0 = present; 1 = absent.



TEXT-FIG. 3. Position of choanae anterior border: A, at the level of P4-M1 of *Merychippus* (drawing from FAM 12793); B, posterior to P4-M1 of *Equus* (redrawn from Eisenmann *et al.* 1988; fig. 6).

TEXT-FIG. 4. Upper teeth characteristics. A, *Equus*; B, *Merychippus*. Redrawn from Eisenmann *et al.* (1988).



4. Muzzle length (Text-fig. 2). This character is determined by comparing I3-P2 diastema length (UDL) and upper tooth-row length (UTRL). Hulbert (1988*b*) recognized five character states. In our case we considered two character states because we analysed a different group of horses.

Outgroup comparison. Hippotheriini horses have a long muzzle, which is regarded as primitive (character state 0).

States. 0 = long (UDL > 40 per cent. of UTRL); 1 = short (UDL < 40 per cent of UTRL).

5. Position of choanae anterior border (Text-fig. 3). The tendency for the retraction of choanae position is related to the lengthening of the face.

Outgroup comparison. All *Merychippus* species and the primitive group of Hippotheriini (morphotypes 1 and 2 *sensu* Alberdi 1989) present the choanal anterior border at the level of P4-M1 or more forward, which is considered primitive.

States. 0 = to level P4-M1 or forward; 1 = posterior to P4-M1.

6. Protocone connection (Text-fig. 4). The protocone condition has been used to subdivide mesodont and hypsodont horses (Stirton 1940). In most recent papers, this character has been used to distinguish the Hippotheriini and Equini tribes (Evander 1989; MacFadden 1992).

Outgroup comparison. The protocone is isolated in all Hippotheriini species (Eisenmann *et al.* 1988).

States. 0 = isolated; 1 = connected.

7. Protocone shape on P3-M2 (Text-fig. 4). In the upper cheek teeth, the protocone varies from rounded, with an anterior spur, to oval and elongated and sometimes with angular borders. To employ this character for taxonomy, we compared the specimens at similar wear stages (Gromova 1952; Alberdi 1974; Eisenmann 1980).

Outgroup comparison. Protocone shape is round to oval in the tribe Hippotheriini.

States. 0 = round; 1 = oval; 2 = elongate-oval; 3 = triangular.

8. Internal postfossette plication (Text-fig. 4). Enamel plication is development in the anterior and posterior walls of prefossettes and postfossettes respectively. The plication decreases during ontogeny (Alberdi 1974). To employ this character for taxonomy we chose anterior postfossette plication because it is more stable. Nevertheless, specimens at similar wear stage were used.

Outgroup comparison. All *Merychippus* species and the most primitive groups of Hippotheriini have simple plication, which is regarded as primitive.

States. 0 = simple; 1 = multiple.

9. Metastyle development (Text-fig. 4). This is observed especially on P3-P4 at middle wear stages.

Outgroup comparison. Most Hippotheriini have a simple metastyle; the derived species have some developed but not to the degree of the Equini tribe (Hulbert 1988b).

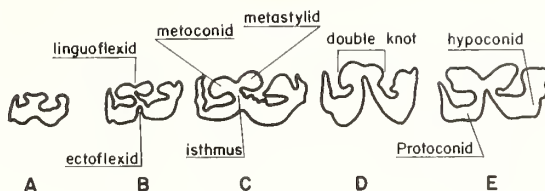
States. 0 = simple; 1 = well-developed.

10. Protocone lingual border. This is observed especially on P3-M2 at middle wear stages. Text-figure 4 illustrates a sample of protocone lingual border.

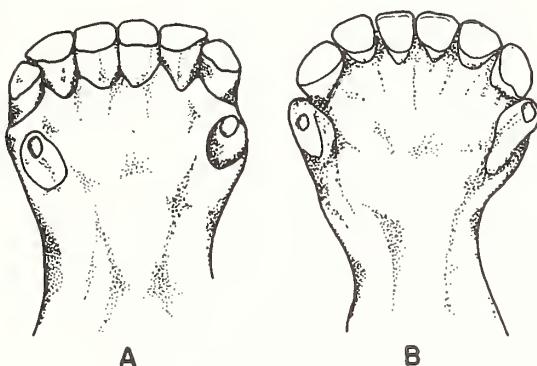
Outgroup comparison. The most derived Hippotheriini species (morphotype 6 *sensu* Alberdi 1989) have a straight or concave lingual border to the protocone (Hulbert 1988b). A round or convex state is regarded as primitive.

States. 0 = round or convex; 1 = straight or concave.

TEXT-FIG. 5. Lower teeth characteristics. A, *Merychippus*; B, *Protohippus*; C, *Pliohippus*; D, *Hippidion*; E, *Equus*.



TEXT-FIG. 6. Lower symphyseal dentitions. A, *Calippus*, with diastema i3-c and linear arcade; B, *Pliohippus*, without diastema i3-c and arcuate arcade.



11. Molar crown height. The increase in height of the tooth crowns was classically related with the change from browsing (brachydont) to grazing (hypsodont) horses (Simpson 1951). The height is taken from the crown bottom to the parastyle top in M1-M2, only in unworn specimens. In the Equini tribe, we think it is important to mark the state of character that reflects the change from browsing to grazing. The molar crown height of more than 28 mm indicates hypsodont horses.

Outgroup comparison. All *Merychippus* species have molar crown heights of about 25 mm (Hulbert 1988a, 1988b; Hulbert and MacFadden 1991). A molar crown height of less than 28 mm is regarded as primitive.

States. 0 = < 28 mm; 1 = $\geq$ 28 mm.

12. Depth of linguaflexid. Shape and depth of the linguaflexid varies with wear. The depth is taken on p3-p4 with middle wear (Text-fig. 5). This character seems more variable because the size of double-knots can be small or very big in relation to the tooth size (character 14).

Outgroup comparison. *Merychippus* has a shallow linguaflexid, which is regarded as primitive (see Text-fig. 5A).

States. 0 = shallow, as in Text-figure 5A morphology; 1 = middle, as in Text-figure 5B and 5D morphologies; 2 = deep, as in Text-figure 5C and 5E morphologies.

13. Depth of the ectoflexid (Text-fig. 5). This character varies with wear. The ectoflexid grooves from the buccal side continue inside and sometimes divide the isthmus into an anterior and a posterior part. The depth is taken on p3-p4 (Alberdi 1974; Hulbert 1988b; Watabe 1992).

Outgroup comparison. All Hippotheriini have a shallow ectoflexid, which is regarded as primitive.

States. 0 = shallow, as in Text-figure 5A morphology; 1 = moderate, without penetrating the isthmus, as in Text-figure 5B and 5D morphologies; 2 = deep, penetrating the isthmus, as in Text-figure 5C and 5E morphologies.

14. Sizes and shapes of the metaconid and the metastylid (Text-fig. 5). The metaconid and metastylid shape on the lower cheek was considered by Gromova (1952), who recognized two morphological types: hipparionid and caballoid. The linguaflexid affects this feature, classically named the double-knot. In the Equini tribe the size and shape of the linguaflexid give the peculiar morphology to the double-knot.

Outgroup comparison. *Merychippus* has small metaconid and metastylid, which is regarded as primitive.

States. 0 = small, as in Text-figure 5A; 1 = of medium size, as in Text-figure 5B–D; 2 = large, as in Text-figure 5E.

15. Buccal borders of the protoconid and the hypoconid (Text-fig. 5). There is no variation during ontogeny (Alberdi 1974; Hulbert 1988b; Watabe 1992).

Outgroup comparison. Hippotheriini has a rounded condition; only the most derived species (morphotype 6 *sensu* Alberdi, 1989) show a tendency to straight protoconid and hypoconid labial borders.

States. 0 = rounded; 1 = straight.

16. Diastema i3-c (Text-fig. 6). Many horses possess a characteristic diastema between i3 and c. This character is mentioned by Bennett (1980).

Outgroup comparison. All *Merychippus* species do not present diastema between i3 and c. An absent diastema i3-c is regarded as primitive.

States. 0 = absent; 1 = present.

17. Incisor arcade (Text-fig. 6). The first and second incisors are arranged in a straight line or in an arcuate line. This feature is mentioned by Hulbert (1988a). Several papers have examined the muzzle and incisor morphologies in relation to dietary preference (e.g. Owen-Smith 1985; Janis and Ehrhardt 1988). These studies have shown that horses adapted to browsing habits had a relatively narrow muzzle and a strongly curved incisor arcade. At the other end of the morphological spectrum, most grazing species had a very broad muzzle, wide symphysis and a linear arrangement of incisors (MacFadden 1992, p. 241). Within fossil *Equus*, several different incisor and muzzle morphologies evolved, but *Equus simplicidens*, considered here, presents the arcuate state.

Outgroup comparison. Hippotheriini has an arcuate arcade, which is regarded as primitive.

States. 0 = arcuate; 1 = linear.

18. Muzzle width relative to upper tooth-row length at moderate wear-stage. This character is mentioned by Hulbert (1988a, 1989). The grazing ungulates have relatively broader muzzles in contrast with browsers. In general, dietary selectivity is related to muzzle width (MacFadden 1992). This character distinguishes *Protohippus* and *Calippus* from the other Equini horses.

Outgroup comparison. Hippotheriini has a narrow muzzle (Hulbert 1989), which is regarded as primitive.

States. 0 = moderate or narrow; 1 = broad (> 36 per cent.).

19. Number of digits. The pentadactyl limb has traditionally been recognized as the tetrapod archetype. Reduction of lateral metapodials in the evolution of horses has been mentioned by several authors (e.g. Matthew 1926; Simpson 1951) in relation to the development of the monodactyl limb.

Outgroup comparison. Hippotheriini species have a tridactyl condition. Loss of digits is derived. Classical ontogenetic studies on the development of the carpus of horses support this polarity (Ewart 1894a, 1894b).

States. 0 = tridactyl; 1 = monodactyl.

20. Gracility of metapodials. The morphological characters in metapodials are closely associated with body weight and functional locomotion and their modifications throughout the evolutionary lineages of horses have been mentioned (Camp and Smith 1942; Sondaar 1968; Alberdi 1974; Hussain 1975; Alberdi and Prado 1993; Prado and Alberdi 1994). The slenderness index was defined by Gromova (1952) as the ratio percentage of the minimum breadth (near the middle of the bone) and the maximum length.

Outgroup comparison. All *Merychippus* species have slender metapodials, which are regarded as primitive.

States. 0 = slender, when the slenderness index is < 15; 1 = robust, when the slenderness is > 15.

Methods

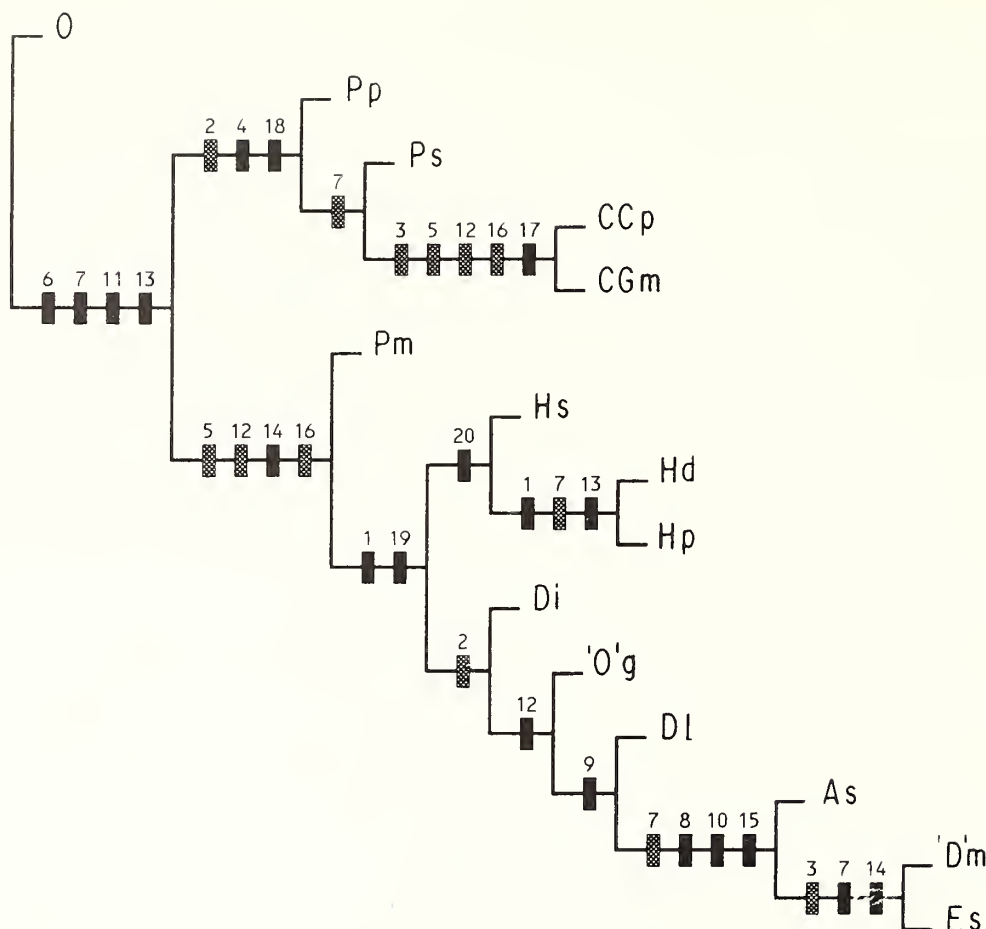
We have used the method of phylogenetic systematics developed by Hennig (1966). All characters are treated as additive, i.e. the transformation sequences are considered to be linear. Table 1

TABLE 1. Data matrix.

Taxa	Characters																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Protohippus supremus</i>	0	1	0	1	0	1	2	0	0	0	1	0	1	0	0	0	0	1	0	0
<i>Protohippus perditus</i>	0	1	0	1	0	1	1	0	0	0	1	0	1	0	0	0	0	1	0	0
<i>Plihippus mirabilis</i>	0	0	0	0	1	1	1	0	0	0	1	1	1	1	0	1	0	0	0	0
<i>Hippidion devillei</i>	2	0	0	0	1	1	2	0	0	0	1	1	2	1	0	1	0	0	1	1
<i>Hippidion principale</i>	2	0	0	0	1	1	2	0	0	0	1	1	2	1	0	1	0	0	1	1
<i>Hippidion saldiasi</i>	?	?	?	?	?	1	?	?	0	0	1	1	1	1	0	?	0	?	1	1
<i>'Onohippidium' galushai</i>	1	1	0	0	1	1	1	0	0	0	1	2	1	1	0	1	0	0	1	0
<i>Dinolhippus interpolatus</i>	1	1	0	0	1	1	1	0	0	0	1	1	1	1	0	1	0	0	1	0
<i>Dinolhippus leidyani</i>	1	1	0	0	1	1	1	0	1	0	1	2	1	1	0	1	0	0	1	0
<i>'Dinolhippus' mexicanus</i>	?	1	1	0	1	1	3	1	1	1	1	2	1	2	1	1	0	0	1	0
<i>Astrohippus stocki</i>	1	1	0	0	1	1	2	1	1	1	1	2	1	1	1	1	0	0	1	0
<i>Calippus (Calippus) placidus</i>	0	1	1	1	1	1	2	0	0	0	1	1	1	0	0	1	1	1	0	0
<i>Calippus (Grammohippus) martini</i>	0	1	1	1	1	1	2	0	0	0	1	1	1	0	0	1	1	1	0	0
<i>Equus simplicidens</i>	1	1	1	0	1	1	3	1	1	1	1	2	1	2	1	1	0	0	1	0

contains the data matrix used in this analysis. The data were analysed using Hennig86 version 1.5 (Farris 1988) for parsimony analysis and CLADOS version 0.9 (Nixon 1991) for examining the character distribution and production of publishing figures. Hennig86 was run with the implicit enumeration option ('ie') for calculating trees.

We rank a fossil's stratigraphical position based on the radiometric dates of the first occurrence following the method proposed by Norell and Novacek (1992a, 1992b) to analyse the consensus between the fossil record and cladistic results. This method is based on that of Gauthier *et al.* (1988). We used the Spearman rank correlation coefficient (Hollander and Wolfe 1973) to measure the fit



TEXT-FIG. 7. Cladogram resulting from analysis of the character matrix in Table 1. Character numbers above the hashmarks correspond to the variables explained in the text. Filled hashmarks indicate non-homoplastic steps; grey patterned hashmarks denote convergences.

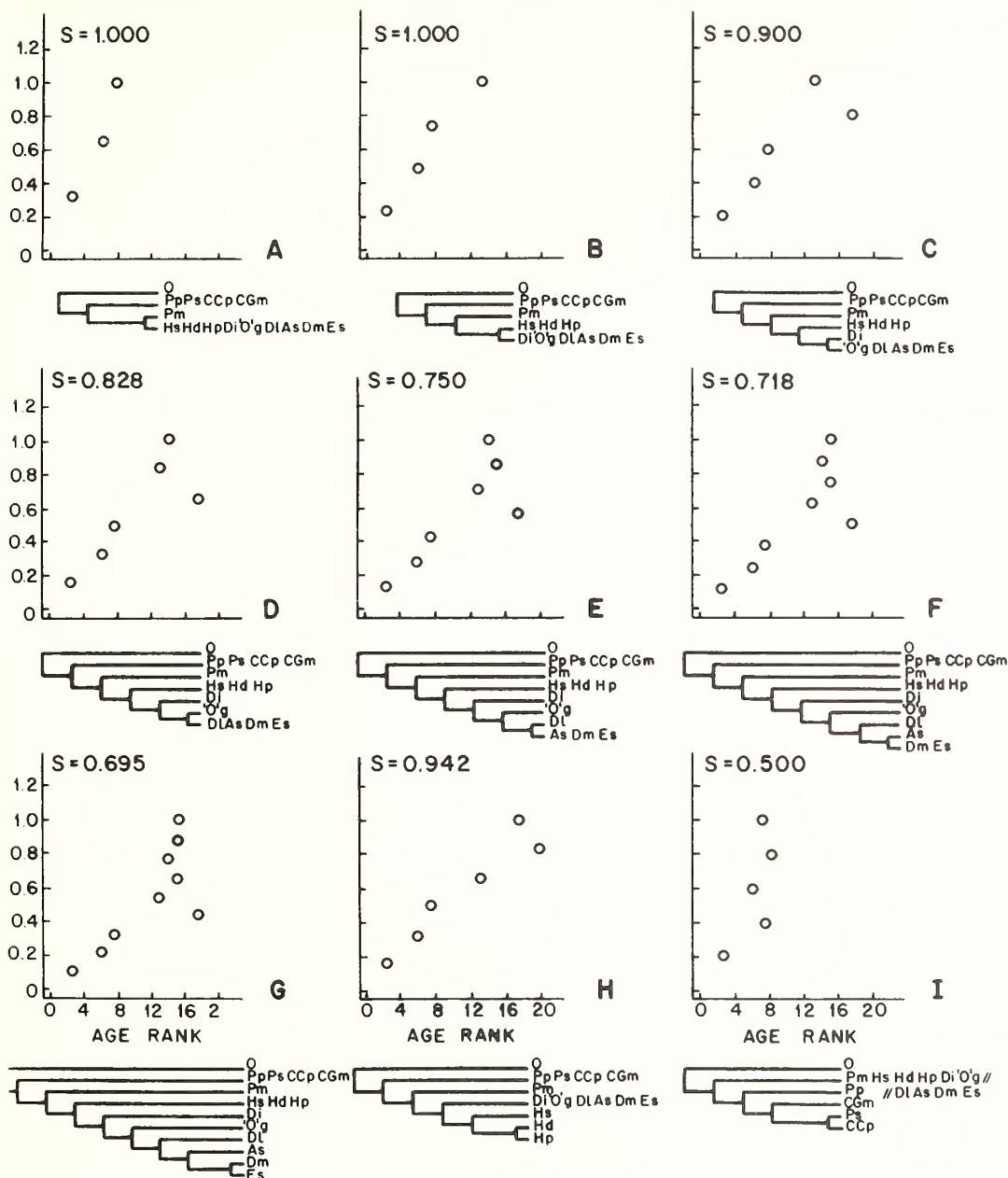
between the fossil record and rank clade in the cladograms (order of branching, with the first branch off of the main spine having the lowest clade rank). This coefficient was calculated using STATGRAPHICS version 5.0 (1991).

RESULTS

The data matrix (Table 1) contains two synapomorphies for the entire tribe (characters 6 and 11) which were not considered for calculations of tree length and consistency index. One parsimonious cladogram of 31 steps and a consistency index of 0.77 was obtained (Text-fig. 7). The cladogram shows that characters from cranial morphology (2, 3 and 5) reflect more parallel evolution.

The tribe Equini presents four synapomorphies: 'protocone connection' [6]; 'shape of protocone' [7]; 'height of molar crown' [11]; and 'depth of ectoflexid' [13]. Two of the four transformation series (7 and 13) present further changes in the cladogram.

The basal node shows two major clades. *Protohippus perditus*, *Protohippus supremus*, *Calippus* (*Calippus*) *placidus* and *Calippus* (*Grammohippus*) *martini* form a first monophyletic group supported by the following synapomorphies: 'short muzzle' [4(1)]; and 'broad muzzle' [18(1)]. There is another character state that supports this group: 'presence of malar fossa' [2(1)], which is



TEXT-FIG. 8. Simple pectinate phylogeny of Equini taxa and plots of age rank versus clade rank for pectinate cladograms (*sensu* Norell and Novacek 1992a, 1992b). Clade ranks are rescaled from 0 to 1. S, Spearman coefficient; O, outgroup; Pp, *Protohippus perditus*; Ps, *Protohippus supremus*; CCp, *Calippus* (*Calippus*) *placidus*; CGm, *C. (Grammohippus) martini*; Pm, *Pliohippus mirabilis*; Hs, *Hippidion saldiasii*; Hd, *Hippidion devillei*; Hp, *Hippidion principale*; Di, *Dinohippus interpolatus*; 'O'g, *'Onohippidion' gahushai*; Dl, *Dinohippus leidyani*; As, *Astrohippus stocki*; Dm, *'Dinohippus' mexicanus*; Es, *Equus simplicidens*.

also found as a synapomorphy in the other major clade. *Calippus* species form a natural group defined by the 'DPOF absent' [3(1)], 'choanae anterior border posterior to P4-M1' [5(1)], 'middle linguaflexid' [12(1)], 'diastema i3-c' [16(1)] and 'linear incisor arcade' [17(1)].

The rest of the species forms a second monophyletic group supported by the following synapomorphies: 'choanae anterior border posterior to P4-M1' [5(1)], 'middle linguaflexid' [12(1)], 'metaconid and metastylid middle' [14(1)] and 'diastema i3-c present' [16(1)] where characters 12 and 14 present a further change in the cladogram. *Pliohippus mirabilis* are sister species of the main group. The other main group is well defined by the following synapomorphies: 'nasal notch between P2 and M1' [1(1)]; and 'monodactyl limb' [19(1)].

Inside this main group, two clades are well defined by synapomorphies. One clade supported by 'robust metapodials' [20(1)] includes the *Hippidion* species from South America. *Hippidion devillei* and *Hippidion principale* are characterized by 'nasal notch posterior to M1' [1(2)], 'elongate-oval protocone' [7(2)] and 'ectoflexid deep, penetrating the isthmus' [13(2)]. The other clade is supported by 'presence of malar fossa' [2(1)]. '*Onohippidium*' *galushai*, *Dinohippus leidymanus*, *Astrohippus stocki*, '*Dinohippus*' *mexicanus* and *Equus simplicidens* form a monophyletic group based on 'deep linguaflexid' [12(2)]. *Dinohippus leidymanus*, '*Dinohippus*' *mexicanus* and *Equus simplicidens* form a natural group supported by the 'well-developed metastyle' [9(1)]. *Astrohippus stocki*, '*Dinohippus*' *mexicanus* and *Equus simplicidens* form a clade characterized by 'elongate-oval protocone' [7(2)], 'multiple internal postfossette plication' [8(1)], 'straight or concave protocone lingual border' [10(1)] and 'straight labial border of protoconid and hypoconid' [15(1)]. Within this clade, '*Dinohippus*' *mexicanus* and *Equus simplicidens* are a monophyletic group based on the 'DPOF absent' [3(1)], 'triangular protocone' [7(3)] and 'large metaconid and metastylid' [14(2)].

We observed a good congruence between the fossil record and the phylogenetic hypothesis. Using our cladogram, nine possible pectinate cladograms have been obtained. Text-figure 8 shows the nine cladograms and the bivariate plots for each clade rank and age rank (A-I). Spearman coefficients are calculated and the results compared in Text-figure 8. Statistically significant correlations ($P < 0.05$) are found in five of the nine examined cladograms (A-B and F-H in Text-fig. 8). The close fit is particularly notable in Text-figure 8A-B and H. The last includes one non-resolved point (Text-fig. 8H), because *Hippidion* from South America is thought to have branched off very early in Equini phylogeny, but appears late in the record (Alberdi and Prado 1993).

DISCUSSION

The different kinds of characters used in the analysis (cranial, upper and lower teeth, mandible and appendicular skeleton morphology) define taxa at different levels in the cladogram. Characters mostly from the cranial morphology and upper teeth characterize the suprageneric taxa. Only synapomorphies of the upper dental morphology supported the tribe Equini. In addition, analysis shows that characters from cranial morphology suffer more parallel evolution and reversals, while characters from the appendicular skeleton, mandible, upper and lower teeth show little homoplasy. This suggests that the cranial morphology could be less conservative than the other features.

Based on phylogenetic information, we propose dividing the tribe Equini into two subtribes: *Protohippina sensu* Hulbert (1988a) and *Pliohippina* (= *Equinae sensu* Gidley 1907 and *Equina sensu* Hulbert and MacFadden 1991). The former includes two genera: *Protohippus* and *Calippus*, and the latter includes five genera: *Pliohippus*, *Hippidion*, *Dinohippus*, *Astrohippus* and *Equus*. Text-figure 7 shows the synapomorphies of cranial and upper teeth morphology that support these subtribes. In the latter subtribe, our analysis differentiated between two lineages, one that gave rise to *Hippidion* and the other to *Equus*.

Protohippus, previously placed as a subgenus of *Merychippus* (Stirton 1940), is now considered to be a valid genus, closely related to *Calippus*. These two genera form a monophyletic group (Hulbert 1988a). Several authors (Stirton 1940; Simpson 1951), have suggested *Protohippus* to be the ancestor of *Pliohippus* and *Equus*; however, our analysis does not support this relationship. *Protohippus supremus* is the sister taxon of *Calippus* species.

The subtribe Protohippina forms the sister group to a second monophyletic group, the subtribe Pliohippina. Different phylogenetic relationships have been proposed between the genera *Pliohippus*, *Hippidion*, *Dinohippus*, *Astrohippus* and *Equus*. Stirton (1940) proposed *Astrohippus* as a subgenus of *Pliohippus*. This author recognized two distinct lineages within *Pliohippus* s.l. based on dental characters: *Pliohippus* s.s., closely related to South American horses; and *Astrohippus*, that gave rise to the *Equus* group species. Quinn (1955) showed that neither *Astrohippus* nor *Dinohippus* could be considered as ancestors of *Equus* based on facial and dental morphology. Quinn derived *Equus* separately from his new genus '*Eoequus*'. Sondaar (1968), in his study of the equid manus, found that '*Dinohippus*' *mexicanus* from Yepómera (Lance 1950) was closely related to *Equus* and generally more advanced in monodactyly than *Astrohippus stocki*. Dalquest (1978) suggested a polyphyletic origin of *Equus* based on dental morphology. Bennett (1980) and MacFadden (1984) showed close affinities between '*Dinohippus*' *mexicanus* and *Equus*. Azzaroli (1982, 1988) considered *Dinohippus leidyianus* to be the ancestor of *Equus*.

Based on our phylogenetic analysis, we consider *Pliohippus* to be the sister taxon to *Hippidion*, *Dinohippus*, *Astrohippus* and *Equus*. The three species of *Hippidion*, *sensu* Alberdi and Prado (1993), form a monophyletic group, which is geographically restricted to South America and became extinct late in the Pleistocene. Alberdi and Prado (1993) did not find evidence of a relationship between '*Ouohippidium*' *galushai* and the *Hippidion* group, as suggested by MacFadden and Skinner (1979), and consequently regarded the former species as belonging within the *Dinohippus*-group. Our phylogenetic analysis supports this hypothesis. Within the *Hippidion* clade, *Hippidion saldiasi* is a sister species of *Hippidion devillei* and *Hippidion principale*. This phylogenetic hypothesis does not fit with the biochronology because the most derived *Hippidion* species appeared first in the South America fossil record.

Astrohippus stocki, '*Dinohippus*' *mexicanus* and *Equus simplicidens* form a monophyletic group. Our analysis shows *Astrohippus stocki* to be the sister group of *Equus*-group. We consider '*Dinohippus*' *mexicanus* as belonging within *Equus*-group.

Both subtribes delimited in the analysis show little overlap in their stratigraphical range (Text-fig. 1). Species of *Protohippus* and *Calippus* are frequently encountered across wide areas of North America east of the Rocky Mountains, ranging from Florida to Texas, and south to Honduras (Hulbert 1988a). The extinction of this subtribe at the end of the early Hemphillian (Text-fig. 1) occurred at a time of major reduction in Mio-Pliocene equid diversity (Webb 1977). The shift from tip-toed tridactyl to a monodactyl foot may have taken place at this time, accompanied by the evolution of a special ligamental pattern of the distal foot (Camp and Smith 1942). In the genus *Pliohippus* the side-toes were finally lost. This one-toed condition was, of course, retained in the various descendants of *Pliohippus*, including *Equus* (Simpson 1951). The Pliohippina subtribe represented a second monophyletic radiation of hypsodont equids. This radiation occurred in North America when aridity reached its peak in the Hemphillian and late Pliocene Blancan with the spread of open grassland in the Great Plains, Great Basin, and in the south-west (Shotwell 1961; Webb 1977). Southern members of this clade (*Hippidion*) dispersed into South America after the Great American Biotic Interchange that occurred about 3 Ma (*sensu* Webb 1985) through the isthmus of Panamá (Alberdi and Prado 1993). On the other hand, *Equus* dispersed throughout Eurasia and Africa during the late Pliocene and, also throughout South America at about the mid Pleistocene (Azzaroli 1982, 1992; Bonadonna and Alberdi 1987; Alberdi and Bonadonna 1988; Alberdi *et al.* 1991; Prado and Alberdi 1994). Before the Great American Biotic Interchange both lineages were represented in North America which would be the locus of origin of *Hippidion* and *Equus*. Nevertheless, *Hippidion* remains occur in the South American record stratigraphically below *Equus* remains. The former appeared during the upper Pliocene-lower Pleistocene and the latter in the middle Pleistocene (Alberdi and Prado 1993; Prado and Alberdi 1994). This can be correlated with the existence of two inter-American savannah corridors through South America (Webb 1985). The first was the high-level Andean route, while the second one corresponds to the low-level Eastern route. The existence of these different routes could be a consequence of the different climatic conditions and possibly was also related to shifts in the pasture photosynthesis cycle of carbon

(from C3 to C4 plants) that occurred in grassland communities (Cerling *et al.* 1991, 1993; Cerling 1992). MacFadden *et al.* (1994) pointed out the possibility of a relationship between fossil horse diet and the type of carbon grasses (C3 or C4). Nowadays, the high grassland has C3 plants while lower elevations have C4 plants.

This cladistic analysis is developed independently of biostratigraphical relationships, although this information is implicit in some character polarities. Nevertheless, there exists a high congruence between our cladistic analysis and the fossil record, especially in Text-figure 8H. This confirms (following Norell and Novacek 1992a, 1992b) the correspondence between age and cladistic information in most vertebrate examples. But, in our case, as we noted above, there is one unresolved point. This surely is a consequence of the fact that, in the phylogenetic tree, *Hippidion* occurred earlier than in the fossil record. Consequently, the pectinate cladogram shows a close fit with the fossil record, and cladogram H (Text-fig. 8) may represent the best preliminary hypothesis of Equini tribe history throughout geological time.

TABLE 2. Systematic palaeontology: classification of family Equidae *sensu* Prothero and Schoch (1989, p. 531) and the tribe Equini based on Text-figure 7. We detail only genera and species dealt with in our cladistic analysis. 'Onolhippidium' appears in inverted commas because we do not consider this genus to be valid (Alberdi and Prado 1993).

Family Equidae Gray, 1821
Subfamily Anchitheriinae Leidy, 1869
Subfamily Equinae Gray, 1821
Genus <i>Kalobatippus</i> Osborn <i>in</i> Cope-Matthew, 1915
Genus <i>Archaeolhippus</i> Gidley, 1906
Genus <i>Paralhippus</i> Leidy, 1858
Genus <i>Merychippus sensu stricto</i> Leidy, 1857
Tribe Hippotheriini Bonaparte, 1850
Tribe Equini Gray, 1821
Subtribe Protohippina Hulbert, 1988a
Genus <i>Protohippus</i> Leidy, 1858
<i>Protohippus perditus</i> (Leidy, 1858)
<i>Protohippus supremus</i> Leidy, 1869
Genus <i>Calippus</i> Matthew and Stirton, 1930
subgenus <i>Calippus</i> Matthew and Stirton, 1930
<i>Calippus (Calippus) placidus</i> (Leidy, 1858)
subgenus <i>Grammohippus</i> Hulbert, 1988a
<i>Calippus (Grammohippus) martini</i> Hesse, 1936
Subtribe Pliohippina subtrib. nov.
Genus <i>Pliohippus</i> Marsh, 1874
<i>Pliohippus mirabilis</i> Leidy, 1858
Genus <i>Hippidion</i> Owen, 1869
<i>Hippidion saldiasii</i> (Roth, 1899)
<i>Hippidion devillei</i> (Gervais, 1855)
<i>Hippidion principale</i> (Lund, 1845)
Genus <i>Dinohippus</i> -group Quinn, 1955
<i>Dinohippus interpolatus</i> (Matthew and Stirton, 1930)
' <i>Onolhippidium</i> ' <i>galushai</i> MacFadden and Skinner, 1979
<i>Dinohippus leidyianus</i> (Osborn, 1918)
Genus <i>Astrohippus</i> Stirton, 1940
<i>Astrohippus stocki</i> Lance, 1950
Genus <i>Equus</i> -group Linnaeus, 1858
' <i>Dinohippus</i> ' <i>mexicanus</i> (Lance, 1950)
<i>Equus simplicidens</i> Cope, 1892

CONCLUSIONS

One parsimonious cladogram of 31 steps with a consistency index of 0.77 was produced, from which a classification of the tribe Equini was constructed. The analysis shows that characters mostly from the cranial morphology and upper teeth characterized the suprageneric taxa. As a result of this phylogenetic analysis, we propose the classification of family Equidae shown in Table 2.

We recognize two subtribes: Protohippina and Pliohippina. The first includes two genera: *Protohippus* and *Calippus*; and the second, five genera: *Pliohippus*, *Hippidion*, *Dinohippus*, *Astrohippus* and *Equus* (Text-fig. 7). *Protohippus supremus* is the sister-taxon of *Calippus* species.

The subtribe Protohippina forms the sister-group to a second monophyletic group, the subtribe Pliohippina. The latter represents a second monophyletic radiation of hypsodont equids. Possibly this was as a result of the more arid conditions and the spread of open grassland in North America.

We consider *Pliohippus* to be the sister-group to *Hippidion*, *Dinohippus*, *Astrohippus* and *Equus*. The three species of *Hippidion* form a monophyletic group, which are geographically restricted to South America. In this clade, *Hippidion saldiasi* is a sister-species of *Hippidion devillei* and *Hippidion principale*. However, *H. devillei* appeared first in the South American fossil record. There is no evidence of a relationship between '*Onohippidium*' *gahushai*, from North America, and the *Hippidion* group, from South America. We include '*O.*' *gahushai* in the *Dinohippus*-group. *Astrohippus stocki* was the sister-species of the *Equus*-group, which includes '*Dinohippus*' *mexicanus*.

This cladistic analysis has a high congruence between the stratigraphical record and the phylogenetic hypothesis. The pectinate cladogram H (Text-fig. 8) is a good hypothesis of Equini tribe history throughout geological time.

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TWO EARLY CRETACEOUS SPIRULID COLEOIDS OF THE NORTH-WESTERN CAUCASUS: THEIR SHELL ULTRASTRUCTURE AND EVOLUTIONARY IMPLICATIONS

by LARISA A. DOGUZHAeva

ABSTRACT. The rare phragmocone-bearing coleoids *Adygeya adygensis* gen. et sp. nov. and *Naefia kabanovi* sp. nov. are described from the Aptian of the north-western Caucasus (Russia). They are considered to be the earliest known members of the order Spirulida, belonging to two families, Adygeyidae fam. nov. and Groenlandibelidae, respectively. The siphuncular and shell wall ultrastructures of the coleoids were studied with SEM and compared with those of Recent *Spirula*.

The two coleoids under consideration possess a longiconic shell, a comparatively wide and strongly expanded siphuncle with spherulitic-prismatic connecting rings, a shell wall as thin as the septa, a short final chamber and comparatively long camerae. Both genera lack rostra and a nacreous layer in the shell wall. They differ mainly in the position of the siphuncle and the shape of septal necks.

Ultrastructural studies of the shell wall in *Adygeya*, *Naefia* and *Spirula* lead to the conclusions that in the lineage of Spirulida (1) the shell possesses the outer plate (*sensu* Appellöf 1893) instead of a rostrum, and (2) the shell wall lacks the nacreous layer. On the basis of the high stability of shell wall structure in cephalopod evolution, it is assumed that these structural differences indicate an early divergence of Decabranchia and Belemnioidea, and that the taxa which had a rostrum and a nacreous layer in the shell wall can hardly be interpreted as precursors of the Spirulida lineage.

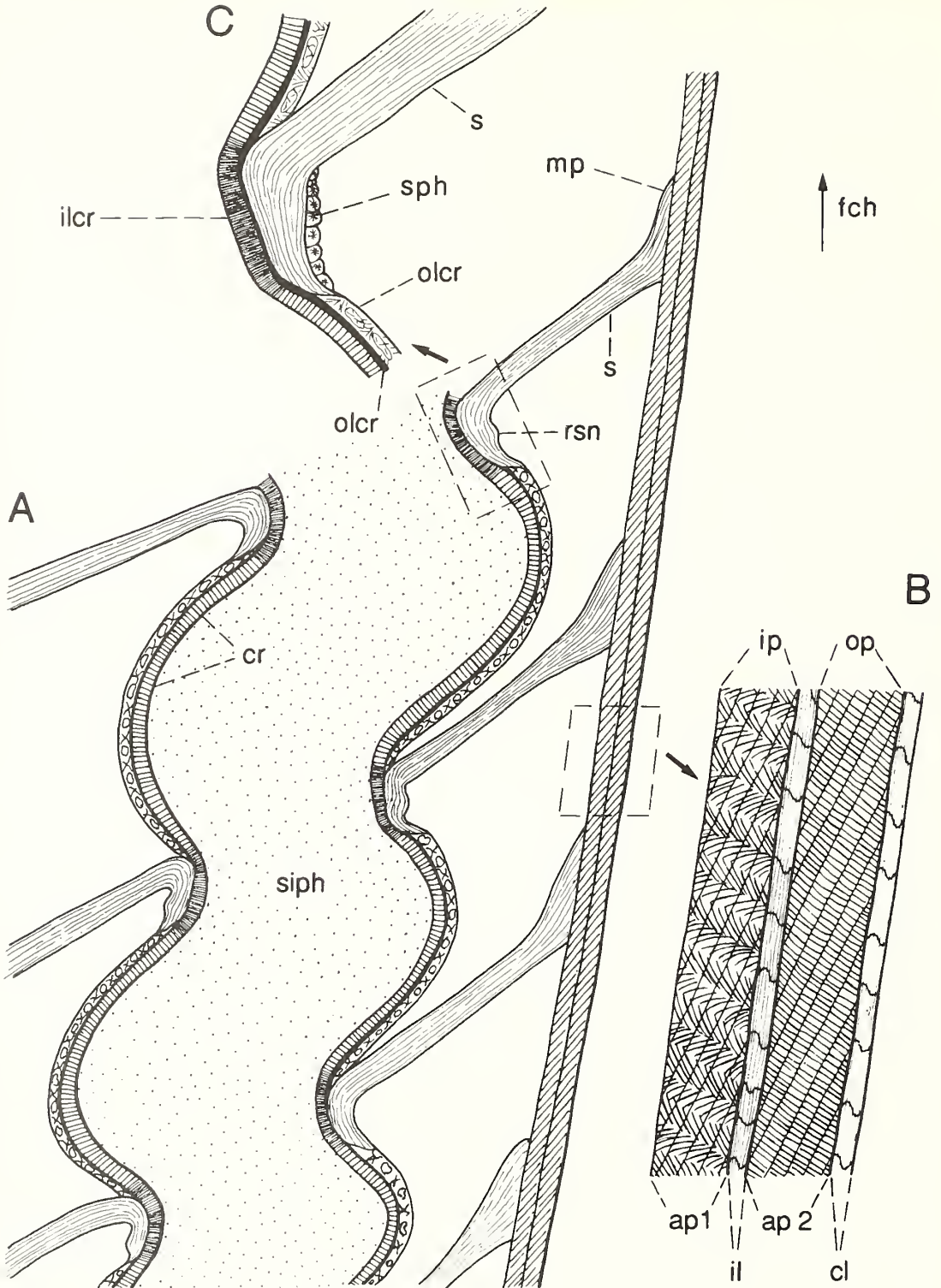
THE Mesozoic record of the spirulids is still inadequately known and until now only two rare taxa were recorded: the Santonian–Maastrichtian *Naefia neogaia*, and the Maastrichtian *Groenlandibelus rosenkrantzi*. The coleoids are markedly similar in phragmocone structure, but different in their pro-ostracum. Comparison at early ontogenetic stages is still lacking as the initial portions of the shell have not yet been described in the former genus.

Naefia, assigned to *N. kabanovi* sp. nov., together with a previously unknown phragmocone-bearing coleoid, here described as *Adygeya adygensis* gen. et sp. nov., were found in Aptian concretions in north-western Caucasus, Russia (in the valley of the Hokodz River in the Belaya River Basin; see Doguzhaeva 1995). Well-preserved shell material of both taxa allowed examination of their shell ultrastructure and comparison of it with that of Recent *Spirula*. The ultrastructural studies of *Naefia* revealed a great similarity of its siphuncle to that in *Groenlandibelus* and gave additional evidence for placement of this genus within the order Spirulida. SEM studies of *Adygeya* showed that its shell wall, being composed of outer and inner plates, is similar to that of Recent *Spirula*, so this genus was assigned to Spirulida also.

PREVIOUS STUDIES

Naefia was previously known from the Campanian–Maastrichtian of Chile (Wetzel 1930; Biro-Bagoczky 1982; Stinnesbeck 1986), Antarctica (Wetzel 1930; Stilwell and Zinsmeister 1987), south India (Doyle 1986) and from the Santonian–Campanian boundary beds of Japan (Hewitt *et al.* 1991). *Groenlandibelus* is known from Upper Maastrichtian of West Greenland (Jeletzky 1966).

Jeletzky (1966) united *Groenlandibelus* and *Naefia* in the family Groenlandibelidae, on the



TEXT-FIG. 1. For caption see opposite.

assumption that *Naefia*, like *Groenlandibelus*, possessed a caecum and a prosiphon. He included (1966, p. 107) this family, together with Spirulidae, in the order Sepiida on the basis of a supposed common ancestry. According to Jeletzky, groenlandibelids represented early specialized sepiids with a longiconic phragmocone and weakly developed (or absent?) rostrum. Donovan (1977, p. 24), however, excluded *Groenlandibelus* and *Spirula* from Sepiida on the basis of the overall morphology of the phragmocone.

Birkelund and Hansen (1974) studied the ultrastructure of the phragmocone, rostrum and septa in *Groenlandibelus* and came to the conclusion that *Groenlandibelus* was an aberrant genus of uncertain taxonomic position. Nevertheless, these authors emphasized that the possession of a caecum and a prosiphon were strong evidence for referring *Groenlandibelus* to Sepiida *sensu* Jeletzky. Later, Reitner and Engeser (1982) followed Donovan (1977) and reintroduced the order Spirulida, in which they included groenlandibelids. *Naefia* was placed by Engeser (1990) in Coleoidea *incertae sedis*, because of the shortage of morphological data in this genus. Doyle *et al.* (1994) placed the family Groenlandibelidae within the order Spirulida which is included by these authors in the superorder Decabranchia.

MATERIAL AND METHODS

The fossil coleoid shells were collected by the author from Aptian sideritic concretions in the valley of the Hokodz River, some 2–5 km below the village of Hokodz, in the Belaya River basin, in the north-western Caucasus (Russia).

The available material comprises: (1) a single phragmocone fragment of *Adygeya* gen. nov. Its maximum diameter is 22 mm and length 20 mm. It includes seven partly preserved septa. It is only slightly altered diagenetically, so the structure of the shell wall, septal necks and connecting rings could be studied in detail. (2) Six fragments of slender orthoconic phragmocones of *Naefia*. The largest phragmocone is 4.5 mm in diameter, and 13 mm in length. It has nine preserved septa, preceding the extremely short final chamber. The smallest phragmocone is 3 mm in diameter, and 9 mm in length. It has seven preserved camerae. The good preservation of this material allowed detailed study of the shell wall, siphuncle and shell/body attachment scars. Some 30 shells of *Spirula* were collected by Dr Moscalev (Institute of Oceanography of the Russian Academy of Sciences) from Cuba.

The following material was studied with SEM: (1) three oblique sections and one median section of the shell in *Adygeya* gen. nov.; (2) medial sections of two phragmocones and the surface of internal moulds of two phragmocones showing dorsal unpaired shell/body attachment scars in *Naefia*; and (3) ten median sections, six cross sections, and five fragments of the fractured shells with exposed inner surface of the camerae at different ontogenetic stages in Recent *Spirula*. To prevent crushing, the latter were embedded in plastic before cutting. Sections were polished with graded diamond pastes, etched for 3–6 seconds with 1 per cent. HCl and coated with gold. The specimens were examined with a Stereo-Scan S4/10 at the Palaeontological Institute of the Russian Academy of Sciences, Moscow and with a Philips SEM 515 at the Swedish Museum of Natural History, Stockholm.

All material listed above is deposited in collection No. 3871 of the Palaeontological Institute of the Russian Academy of Sciences.

TEXT-FIG. 1A–C. *Adygeya adyensis* gen. et sp. nov.; siphuncular tube (A, C) and shell wall (A–B) in median section; A, $\times 20$; B, $\times 100$; C, $\times 35$. Legend to Text-figures 1–3: a, aperture; apl, acicular-prismatic layer of the inner plate; ap2, acicular-prismatic layer of the outer plate; as, attachment scar; aux, auxiliary deposits; cl, coating layer; cr, connecting ring; f, flap; gl, growth lines; il, intermediate layer; ilcr, inner layer of connecting ring; ip, inner plate of shell wall; mp, mural part of septum; mr, mural ridge; nac, nacreous layer; olcr, outer layer of connecting ring; op, outer plate of a shell wall; r, rim; rsn, retrochoanitic septal neck; s, septum; shw, shell wall; siph, siphuncle; sph, spherulitic-prismatic covering of outer surface of septal neck.

GEOLOGICAL SETTING

The studied coleoids were found in concretions together with Aptian ammonoids belonging to the following genera: *Ptychoceras*, *Acanthohoplites*, *Diadochoceras*, *Nodosohoplites*, *Hypacanthoplites* and *Melchiorites*. The concretions also contained ammonoids with a longer stratigraphical range: *Euphyloceras*, *Phyllopachyceras*, *Tetragonites* and *Gabbioceras*. The rest of the cephalopod fauna comprises the belemnite *Mesohibolites*, and the orthocerid *Zhuravlevia* Doguzhaeva, 1995.

The local Aptian strata include sandstones, siltstones and clays with sideritic concretions, c. 0.2–0.5 m in diameter, some containing as many as 20 ammonoid shells. In the sediments, the abundance of quartz gravel, and numerous pieces of carbonized wood, some large, indicates that these sediments were deposited in a nearshore environment (see Doguzhaeva 1995). The Aptian section is well dated by ammonoids, and five ammonoid zones have been proved in the region (Egoyan 1969). The coleoids under consideration occur in the uppermost zone of *Diadochoceras nodosocostatum* and *Acanthohoplites bigoureti*.

TERMINOLOGY

The following terms are used to describe the shell wall structure in *Adygeya*, *Naefia* and *Spirula*.

Coating layer (Text-figs 1B; 2A). This is the outermost lamellar layer of the shell wall consisting of alternate organic and calcified lamellae; it is considered to be secreted from the outside of the final, or body, chamber. It corresponds to the outer portion of the outer plate as described by Appellöf (1893). The term was introduced first to define the lamellar layer covering the shell of the Late Cretaceous ammonite *Gaudryceras* (Druschitc *et al.* 1978). On the basis of the relationship between the coating layer and the shell proper in *Gaudryceras* it was concluded that the shell became internal at an early ontogenetic stage. Thus, the coating layer had a similar origin to that of the rostrum, in being secreted outside the final, or body, chamber. This conclusion was confirmed by Birkelund (1981) and received further attention in shell wall studies of the Early Cretaceous *Ptychoceras* and *Aconeceras* (Doguzhaeva and Mutvei 1989, 1991).

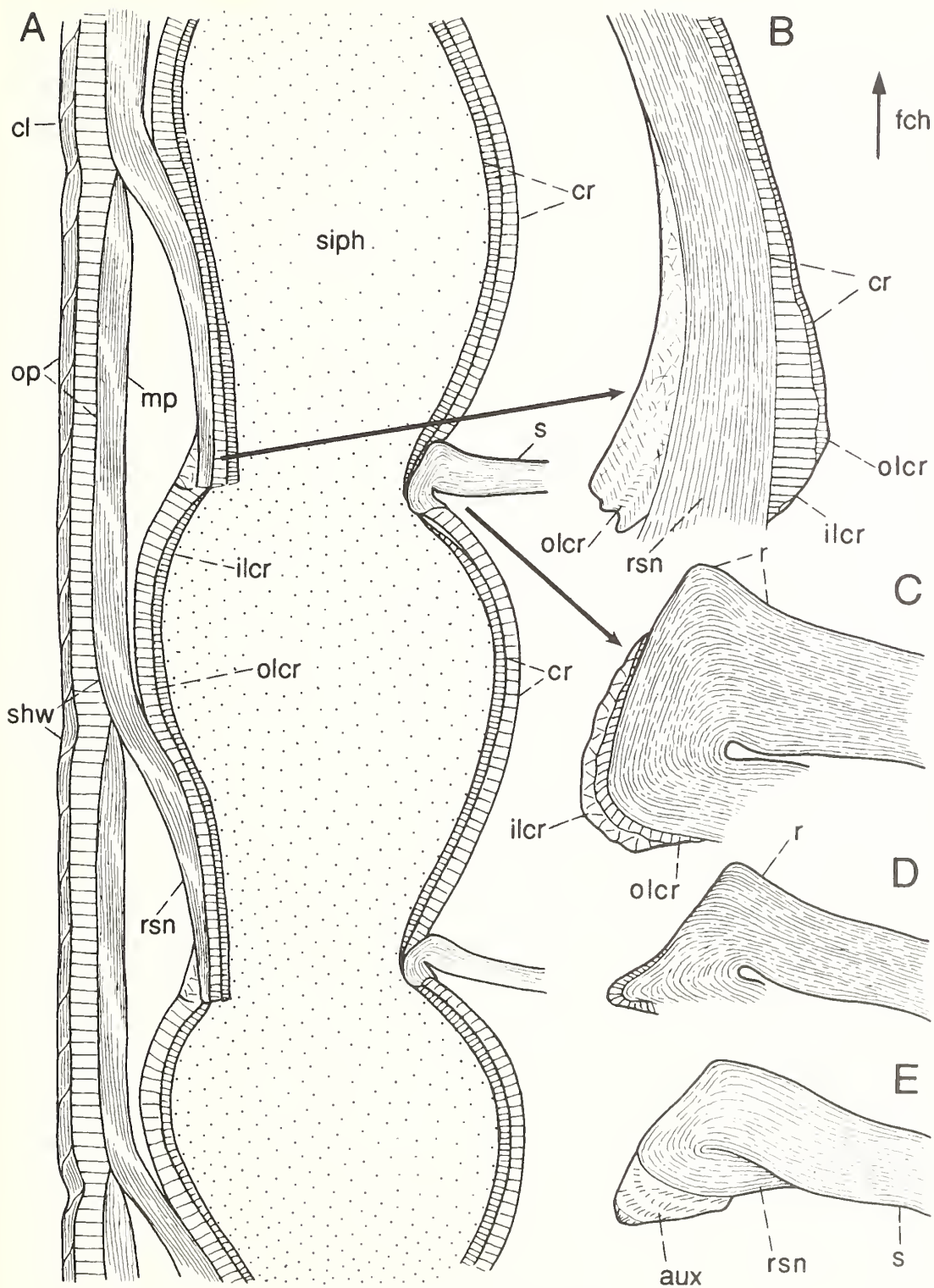
Final chamber. The final portion of the shell between the last septum and the aperture, in ectocochleates it corresponds to the body chamber; in coleoids it houses the rear portion of the body which secretes the septa and the inner part of the shell wall. The term is introduced to emphasize the absence of a chamber which could house the whole body in endocochleate cephalopods.

Guardlike sheath. This is the sheath-like structure of sepiids. According to Jeletzky, who introduced the term, the rostra, tela and guard-like sheaths arose independently in the Belemnitida, Aulacocerida and Tertiary Sepiida. They represent 'convergent evolutionary development resulting in far-reaching homeomorphical similarities of the animals concerned' (Jeletzky 1966, p. 10). The term corresponds to the outer plate of Appellöf (1893).

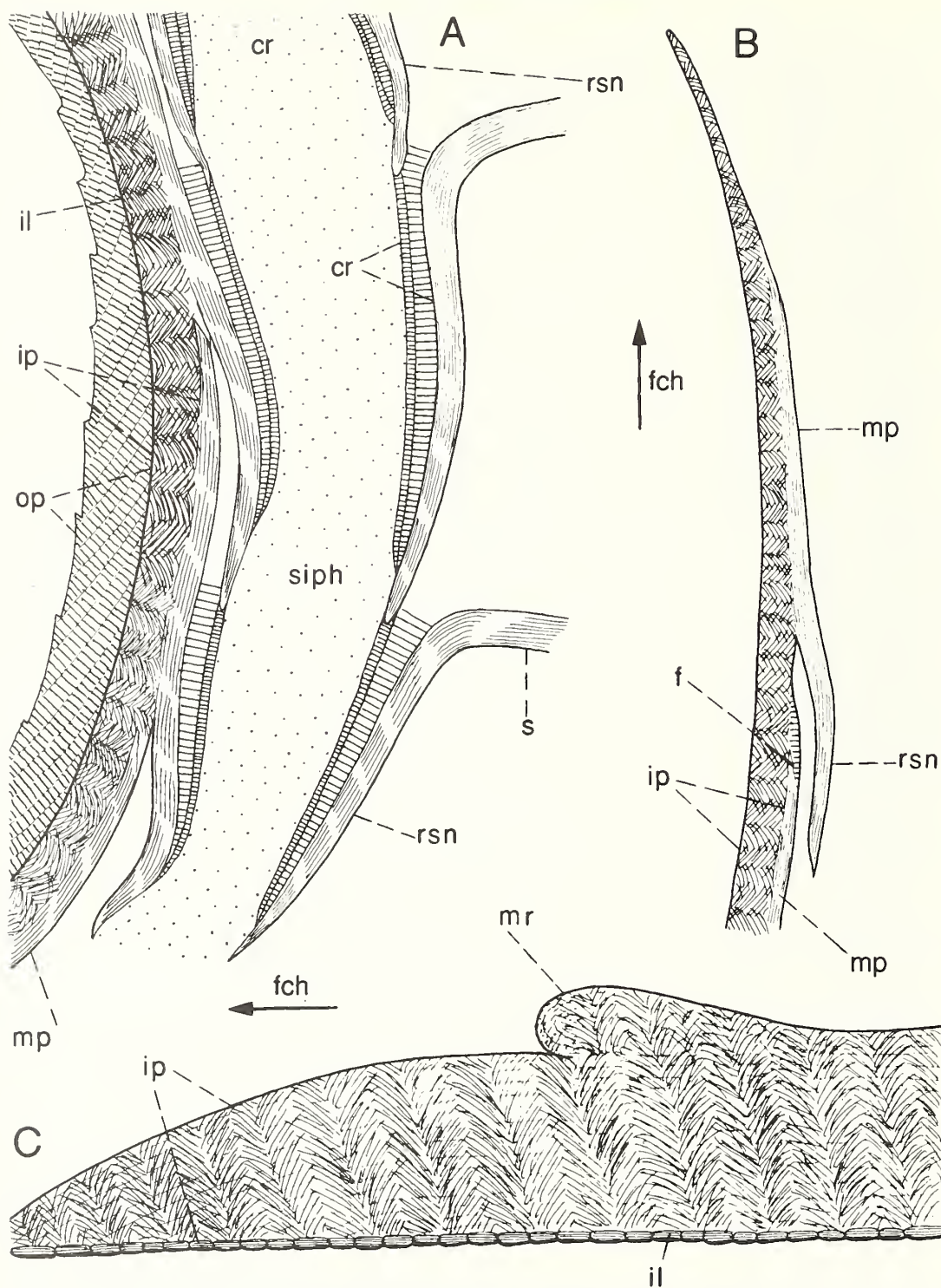
Inner acicular-prismatic layer (Text-figs 1A–C; 3A–B). This is the inner, principal layer of the shell wall characterized by the strongly oblique growth lines and a dendritic pattern formed by acicular crystallites arranged into inclined prisms; it corresponds to the inner plate of Appellöf (1893).

Inner and outer plates (Text-figs 1A–B; 2A, 3A–C). These are the inner and outer portions of the shell wall separated by a distinct interruption. The term was introduced by Appellöf (1893) and applied

TEXT-FIG. 2A–E. *Naefia kabanovi* sp. nov. A, siphuncular tube and shell wall; $\times 70$. B–C, enlarged detail of A: last septal neck from the ventral (B) and dorsal (C) sides; $\times 300$. D, dorsal portion of a septal neck with adorally directed rim; $\times 300$. E, cyrtocoanitic dorsal septal neck; $\times 350$. For legend see caption for Text-figure 1.



TEXT-FIG. 2. For caption see opposite.



TEXT-FIG. 3A-C. *Spirula spirula*. A, siphuncular tube; $\times 70$. B-C, shell wall; B, $\times 60$; C, $\times 180$. For legend see caption for Text-figure 1.



TEXT-FIG. 4A–C. *Naefia kabanovi* sp. nov.; Upper Aptian, River Hokodz, north-western Caucasus. A, 3871/126; lateral view of the phragmocone, with seven preserved camerae; $\times 16$. B, 3871/124, holotype; lateral view of phragmocone, with two visible retrochoanitic septal necks and eight preserved camerae; $\times 14$. C, 3871/125; dorsal view of phragmocone, with shell/body attachment scars (dorsal line); $\times 9$.

to the shell wall of *Spirula*. It emphasizes the distinct separation of the inner and outer portions of the shell. Later, Chun showed that the interruption in the shell wall of *Spirula* is caused by the attachment of the longitudinal muscles near the aperture where the outer plate is still absent; it appears near the fourth camera on the ventral side and at the penultimate camera on the dorsal side (Chun 1898–99, p. 332, fig. 38).

Intermediate layer (Text-figs 1B; 3A–C). This is a predominantly organic, partly calcified layer between the inner and the outer plates of Appellöf, and corresponding to the assumed periostracum in *Spirula* (Mutvei 1964).

Lamello-fibrillar nacre. Each mineral lamella consists of numerous parallel aragonite rods with a different orientation in consecutive lamellae; the intralamellar organic membranes which subdivide the septal nacre into thin mineral lamellae in the ectocochleate cephalopods are absent here; in sections the rods give an impression of a granular structure, in contrast with tabular nacre with its predominantly hexagonal aragonite crystals which in sections look like columns of tabulae. Lamello-fibrillar nacre forms the septa of *Spirula*, *Sepia*, *Naefia*, *Groenlandibelus*, *Adygeya* and belemnites, whereas the tabular nacre composes the septa and the nacreous layer of the shell wall in Recent *Nautilus*, orhoceroids, bactritoids and ammonoids.

Outer acicular-prismatic layer (Text-figs 1A–B; 3A). This is the outer, principal layer of the shell wall, lying outside the intermediate layer. It consists of acicular prisms arranged perpendicular to the growth lines, and it corresponds to the inner portion of the outer plate of Appellöf (1893).

SYSTEMATIC PALAEONTOLOGY

Subclass COLEOIDEA Bather, 1888

Order SPIRULIDA Stolley, 1919

Family ADYGEYIDAE fam. nov.

Type genus. *Adygeya* gen. nov.

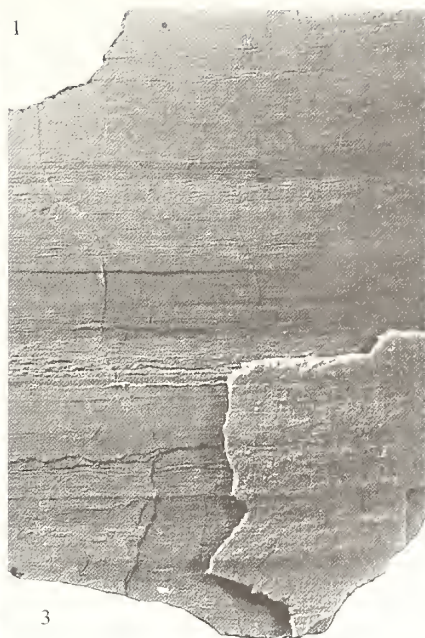
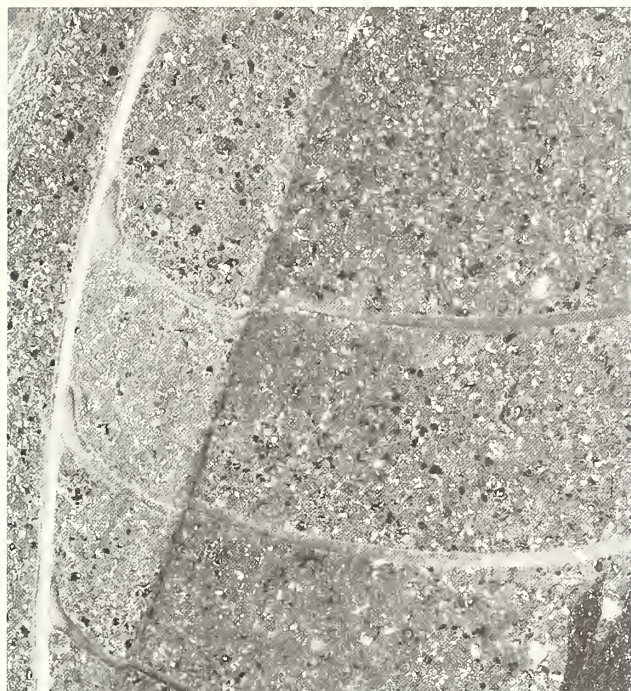
Diagnosis. Shell either orthoconic or slightly exogastrically cyrtconic with comparatively long camerae; rostrum not developed. Surface with thin longitudinal and transverse striations and weak undulations at sutures. Siphuncle comparatively wide, sub-ventral, strongly expanded within camerae. Septal necks short; cyrtchoanitic. Connecting rings thick and calcified. Final chamber short; its length less than the distance between two consecutive septa. Shell wall and septa are of about the same thickness. Shell wall is prismatic, subdivided by the intermediate layer into the inner and outer plates. The inner plate consists of a single acicular-prismatic layer; the outer plate is composed of acicular-prismatic and coating layers.

Range and distribution. Lower Cretaceous, Aptian of the north-western Caucasus.

Remarks. The description is based on the adult shell; early growth stages are unknown. The family is established on the basis of the following features: (1) the orthoconic or slightly cyrtconic

EXPLANATION OF PLATE I

Figs 1–3. *Adygeya adygensis* gen. et sp. nov.; 3871/127; Upper Aptian, River Hokodz, north-western Caucasus. 1, tangential section through phragmocone, showing length of camerae and sub-ventral siphuncle; $\times 8$. 2, detail of fig. 1 showing cyrtchoanitic septal neck; $\times 16$. 3, external view of holotype (ventro-lateral side) with exposed outer surface of inner and outer plates (the fragment of the latter is in the right bottom corner). Uneven longitudinal and transverse striation and weak undulations near septa are visible; the outer plate shows reticulated sculpture; $\times 10$.



phragmocone has a comparatively large diameter; (2) the ventral and dorsal portions of the septal neck are short; (3) the mural parts of the septa are short; (4) the shell wall is prismatic, subdivided by the intermediate layer into the outer and inner plates; and (5) the outer plate consists of the acicular-prismatic and coating layers and the inner plate of the acicular-prismatic layer. In contrast, the family Groenlandibelidae is characterized by: (1) slender phragmocones; (2) long ventral and short dorsal portions of the septal necks; (3) long ventral and short dorsal mural parts of the septa; (4) the absence of a distinct intermediate layer in the shell wall; and (5) the outer plate being represented by a single coating layer, the acicular-prismatic layer being absent. Besides this, the anterior ends of the mural parts of the septa are covered by the innermost portions of the shell wall, in contrast to the condition in the Adygeyidae.

The family is referred to Spirulida because in *Adygeya* as well as in *Spirula* (1) the well-developed phragmocone possesses comparatively long camerae and a wide marginal siphuncle; (2) the final chamber is short; (3) a rostrum is absent; (4) the shell wall is subdivided by the intermediate predominantly organic layer into the inner and the outer plates; and (5) the inner plate is composed of a single acicular-prismatic layer and the outer plate consists of two layers, the acicular-prismatic and coating layers.

Genus ADYGEYA gen. nov.

Derivation of name. From Adygeya, the land of the Circassian native in the north-western Caucasus, where the coleoid was found.

Type species. *Adygeya adyensis* sp. nov.

Type locality. Some 2–5 km below the village Hokodz, in the valley of the Hokodz River, Belaya River Basin, north-western Caucasus.

Horizon. Lower Cretaceous, Upper Aptian (Clansenian).

Diagnosis. The same as for the family.

Adygeya adyensis sp. nov.

Plate 1, figures 1–3; Plate 2, figures 1–4; Plate 3, figures 1–2; Plate 4, figures 1, 4; Plate 5, figures 1–3

Derivation of name. The same as for genus.

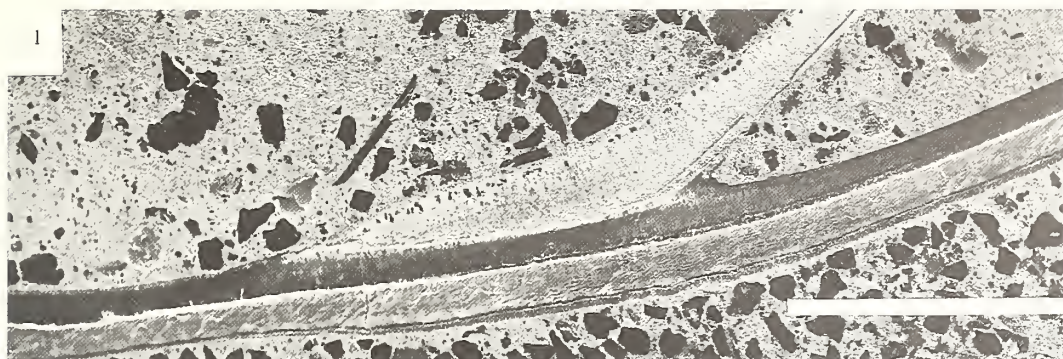
Holotype. 3871/127, in the Palaeontological Institute of the Russian Academy of Sciences.

Type locality. The same as for the genus.

Description. The holotype is a 22 mm long portion of the phragmocone and comprises seven camerae; it is 20 mm in maximum diameter. The shell is an orthocone or a slightly exogastric cyrtocone. In the adult stages there is no evidence for a rostrum. Surface with thin uneven longitudinal and transverse striations and weak undulations near the septa. The comparatively wide siphuncle is sub-ventral, strongly expanding within the camerae. The ratio between the height and width of the siphuncular segments is about 1. Septal foramen oval.

EXPLANATION OF PLATE 2

Figs 1–4. *Adygeya adyensis* gen. et sp. nov.; 3871/127; Upper Aptian, River Hokodz, north-western Caucasus; micrographs of the shell wall in median section. 1, general view of the shell wall, showing inner and outer plates, separated by intermediate layer, and covered by coating layer; scale bar represents 1 mm. 2, detail of fig. 1 showing the indistinct boundary between shell wall and septum, and the continuation of lamellae between them; scale bar represents 0.1 mm. 3, detail of fig. 1, showing porous lamellar structure of the intermediate layer; scale bar represents 0.1 mm. 4, detail of fig. 1, showing coating layer with lamellar structure covering the outer plate; scale bar represents 10 μ m.



Necks are short retrochoanitic. Mural parts of the septa are short. The connecting rings consist of two thick spherulitic-prismatic layers. The adorally preserved camera is about 3.2 mm long along the ventral side; the seventh camera, which is the last preserved, is about 2.2 mm long along the ventral side. Length of the last camera is about 0.1 of its diameter. The final chamber length is estimated as short, less than the length of one camera, on the basis of (1) an absence of the separating boundary between the septa and the shell wall and (2) the strongly oblique growth lines in the inner layers of the shell wall. Both conditions are as observed in *Spirula*. The shell wall consists of the inner and the outer plates, separated by the intermediate layer.

Subclass COLEOIDEA Bather, 1888
Order SPIRULIDA Stolley, 1919
Family GROENLANDIBELIDAE Jeletzky, 1966

Type genus. *Groenlandibelus* Jeletzky, 1966.

Diagnosis. Slender longiconic orthocones with regular contractions near sutures, long camerae and a comparatively wide, ventral siphuncle. Siphuncle begins with a caecum and prosiphon within the protoconch. Ventral mural parts of the septa as long as the distance between the two septa; dorsal parts short. Septal necks retrochoanitic; short cyrtchoanitic dorsally and long holochaoanitic ventrally. The last few septal necks on the dorsal side look to be transitional to prochoanitic. Segments swollen. Connecting rings spherulitic-prismatic. Final chamber short, as long as camerae. Rostrum absent or restricted to the earliest portion of the phragmocone. Shell wall consists of prismatic and coating layers.

Range and distribution. Upper Aptian of north-western Caucasus; Santonian–Campanian boundary of Japan; Campanian–Maastrichtian of Chile, south India, Antarctic Peninsula; Upper Maastrichtian of West Greenland.

Genus NAEFIA Wetzel, 1930

Type species. *Naefia neogaeia* Wetzel, 1930.

Type locality. Chile.

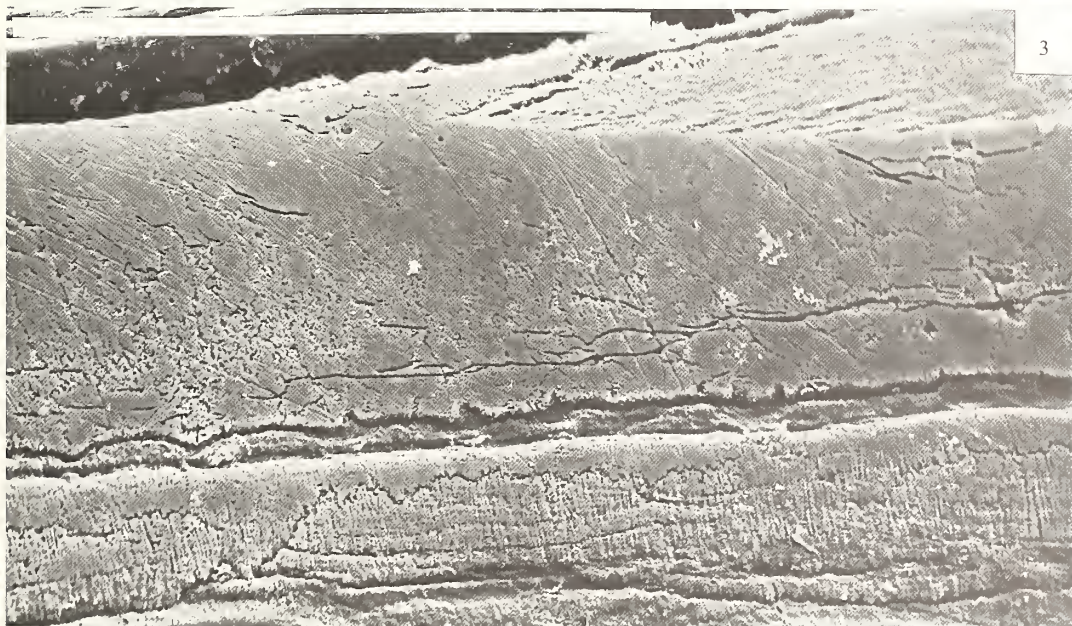
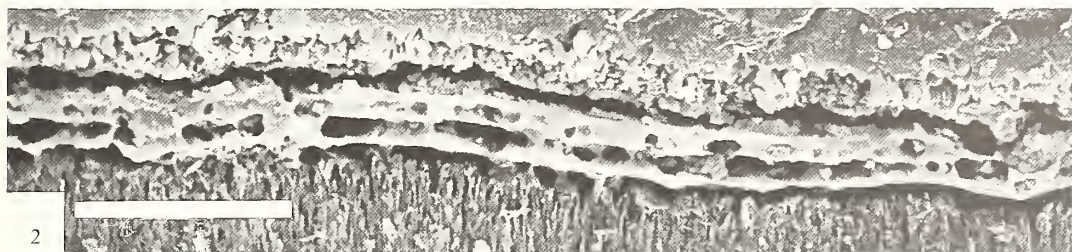
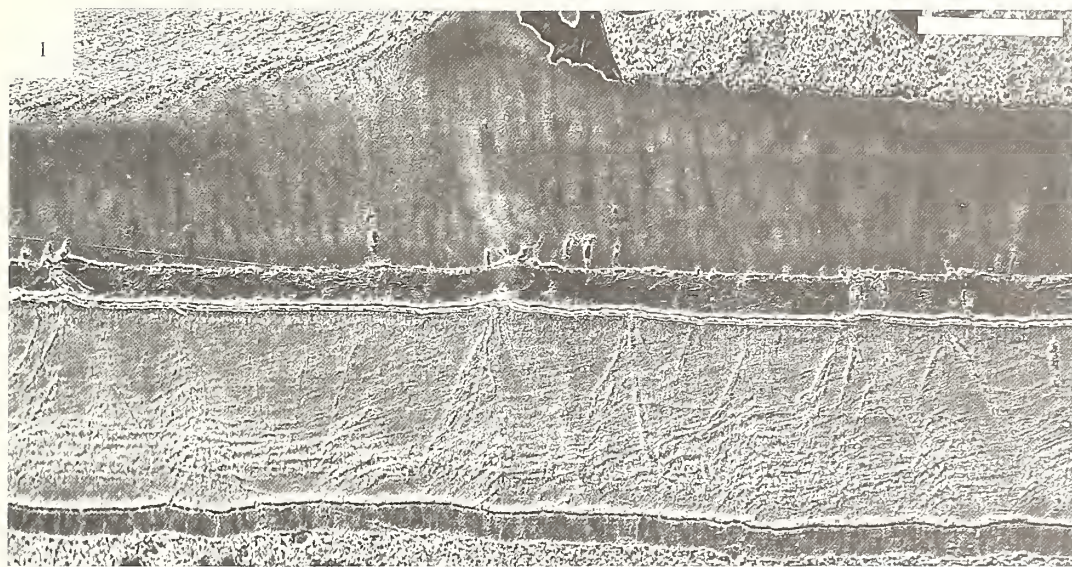
Diagnosis. The same as for the family, with the following additions: dorsal unpaired shell/body attachment scars occur on inner surface of each camera; they are narrow and as long as a camera; pro-ostracum is narrow with broad median field.

Range. Same as for family.

Remarks. Differs from *Groenlandibelus* in the structure of the pro-ostracum: the median field is relatively broad in *Naefia* (Doyle, 1986), but narrow in *Groenlandibelus*. Since early growth stages are not known, the comparison with *Groenlandibelus* cannot be complete. The distinct similarity between *Naefia* and *Groenlandibelus* was pointed out by Birkelund (1956), Jeletzky (1966) and Doyle (1986). The structure of the siphuncle, described here, stresses this resemblance. This justifies the assignment of *Naefia* within the Groenlandibelidae.

EXPLANATION OF PLATE 3

- Figs 1–2. *Adygeya adygensis* gen. et sp. nov.; 3871/127; Upper Aptian, River Hokodz, north-western Caucasus. 1, inner plate (top), intermediate layer, outer plate and coating layer of the shell wall (see also Pl. 2, fig. 1); scale bar represents 0.1 mm. 2, detail of fig. 1 showing the organic lamellae within the intermediate layer. Scale bar represents 10 μ m.
Fig. 3. *Spirula spirula*; 3871/128; Cuba; shell wall, showing inner and outer plates, separated by intermediate layer; scale bar represents 0.1 mm.



Naefia kabanovi sp. nov.

Plate 6, figures 1–5; Plate 7, figures 1–2; Plate 8, figures 1–4; Plate 9, figures 1–3; Text-figure 4

Derivation of name. In honour of G. K. Kabanov, the expert in Cretaceous belemnites, to whom I am grateful for the joint expeditions to the Volga River region.

Holotype. 3871/124, in the Palaeontological Institute, Russian Academy of Sciences.

Type locality. Some 2–5 km below the village Hokodz, Hokodz River valley, Belaya River Basin, north-western Caucasus.

Description. Slender longiconic orthocones, circular in cross section. Angle of expansion 12–14° at early ontogenetic stages to 7–9° at adult stage. Shell surface with fine, uneven longitudinal and transverse striations, and weak undulations near sutures. Inner ventral shell surface with regular contractions at intervals equal to number of camerae. Camerae long, about 30 per cent. of the shell diameter. Sutures normal, with small ventral and dorsal lobes. Siphuncle wide, expanded within camerae, ventral: submarginal at early ontogenetic stages then marginal. Siphuncular diameter is about 20 per cent. of that of the phragmocone at the septal necks; diameter of the septal foramen is about 65 per cent. of the siphuncular segment. The ratio of segment length to maximum diameter is about 1.3–1.5 to 1.0. Septal necks retrochoanitic, short cyrtochoanitic dorsally and long subholochoanitic ventrally. The last few septal necks on the dorsal side look transitional to prochoanitic due to a thickened, adoral rim. Connecting rings consist of two spherulitic-prismatic layers. Mural parts of septa are short dorsally and as long as the camerae ventrally. Final chamber is short, its length equal to the distance between two consecutive septa. Shell wall prismatic with thin coating layer. It is thicker ventrally than dorsally, the ventral wall together with mural parts of septa being about three times thicker than the dorsal wall. On dorsal side, a thin inner portion of shell wall forms flaps covering mural parts of septa. The flap at the adult aperture is prominent.

Remarks. In *N. kabanovi* the sutures are normal to the shell axis whereas in *N. neogaeia* Wetzel, 1930 they are slightly oblique.

The siphuncular structures in *N. neogaeia*, as well as the shell wall/body attachment scars are not known, so the comparison with the latter is restricted to external morphology and cannot be complete. The pro-ostracum is unknown in *N. kabanovi* but is known in *N. neogaeia*.

SHELL ULTRASTRUCTURE

Previous studies

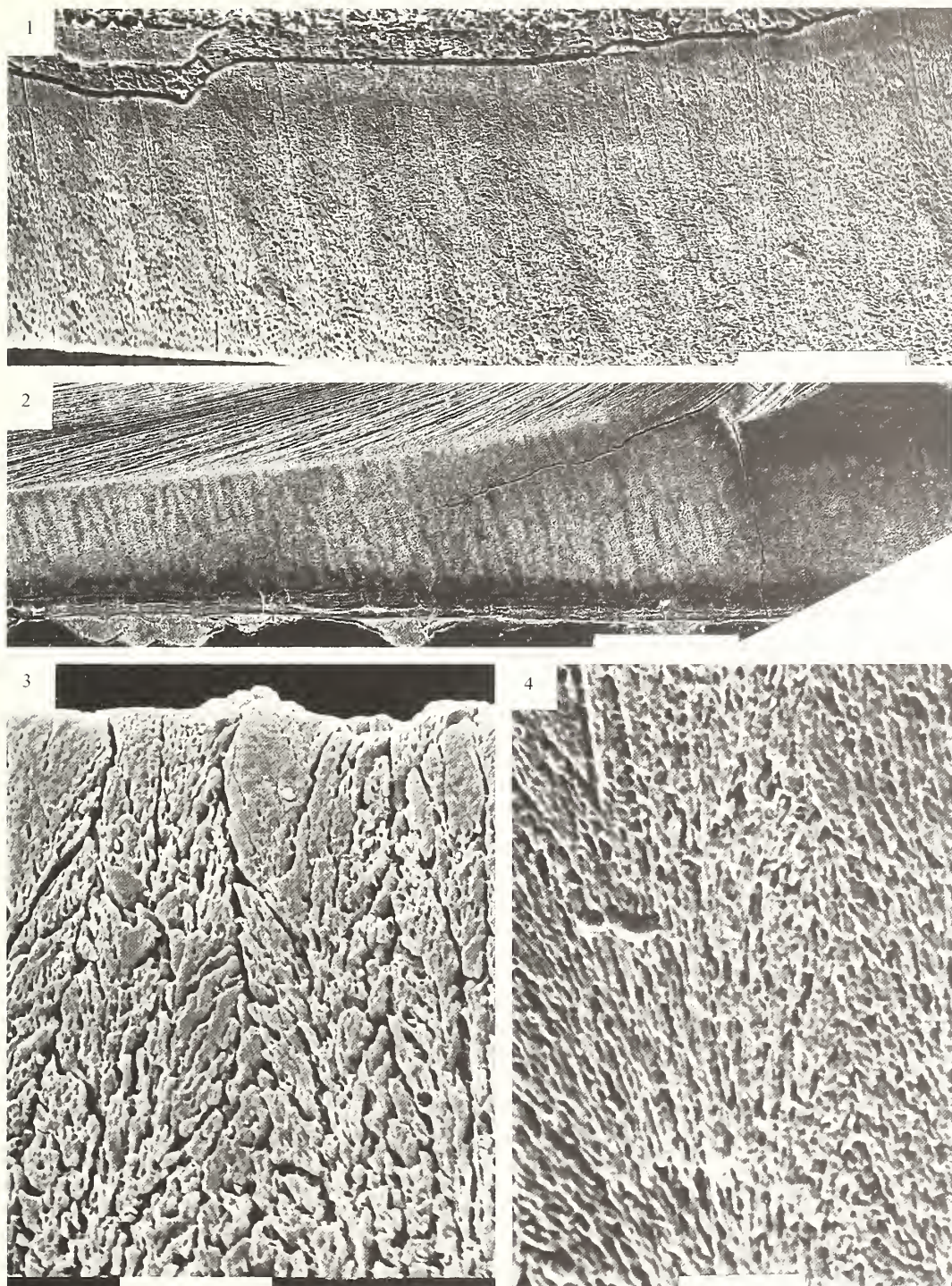
Hewitt *et al.* (1991) found that in *Naefia* the shell wall consists of a thick prismatic layer, invested from outside by a thin lamellar layer which, according to them, could be nacreous. These authors also found that in *Naefia* the septa possess lamello-fibrillar nacre.

Jeletzky (1966) studied the shell structure in the related genus *Groenlandibelus*. According to him, the wall of the phragmocone consists of a prismatic layer, which is more similar in its structure to the internal 'semi-prismatic' layer of the shell in *Spirula* (Mutvei 1964) than to the phragmocone wall in belemnites. In addition, he showed that in *Groenlandibelus* connecting rings are composed

EXPLANATION OF PLATE 4

Figs 1, 4. *Adygeya adygensis* gen. et sp. nov.; 3871/127; Upper Aptian, River Hokodz, north-western Caucasus. 1, inner plate of the shell wall showing oblique vertical bands similar to those in the inner plate of the shell wall in *Spirula* (fig. 2); scale bar represents 0.1 mm. 4, feather-like arrangement of the acicular crystallites within the inner plate, similar to that in *Spirula* (fig. 3); scale bar represents 10 μ m.

Figs 2–3. *Spirula spirula*; 3871/128; Cuba. 2, shell wall, showing inner plate and thin outer plate, separated by intermediate layer; inner plate is similar to that in *A. adygensis* (fig. 1) in showing oblique vertical bands; scale bar represents 0.1 mm. 3, feather-like arrangement of the acicular crystallites within the inner plate, similar to that in *A. adygensis* (fig. 4); scale bar represents 10 μ m.



DOGUZHAEVA, *Adygeya, Spirula*

of two, partly calcified layers; septa are built up of irregularly oriented granulae or spiculae; mural parts possess a considerable amount of organic matter in the calcium carbonate.

Birkelund and Hansen (1974) also studied the shell ultrastructure in *Groenlandibelus*, and compared it with that in the other coleoids. According to them, the nacreous septa are of granular structure, without intralamellar membranes. This feature allies the genus to Belemnitida, while the unilayered, prismatic phragmocone wall allies it to Sepiida.

Shell wall in Adygeya, Naefia and Spirula

Adygeya. The shell wall is preserved on the ventral and ventro-lateral sides. It is characterized by the absence of the nacreous layer (Pl. 3, fig. 1; Text-fig. 1A–B), fine reticular sculpture (Pl. 1, fig. 3) and in being thin (Pl. 1, figs 1–2). By contrast with the ectocochleates, in *Adygeya* the shell wall has approximately the same thickness as the septa. It consists of the inner and the outer plates separated by the intermediate layer (Pl. 2, fig. 1; Text-fig. 1A–B).

1. The inner plate is represented by the inner, principal acicular-prismatic layer. It is about one-third to one-half of the total thickness of the shell wall (Pl. 2, fig. 1). The layer is composed of prisms, about 0.01–0.02 mm wide, with a dendritic structure, formed by a feather-like arrangement of acicular crystallites in each prism (Pl. 4, fig. 4). The growth lines are oblique and oriented approximately at the same angle as those in the outer principal layer. Median sections of this layer show alternation of dark and light, branched vertical bands which are slightly inclined forward (Pl. 3, fig. 1). The orientation of the bands follows the orientation of the long axes along which the crystallites are grouped, forming a dendritic pattern. The bands are assumed to be organic matter between vertical prisms. In addition, in etched preparations, narrow interspaces, probably filled originally by organic matrix, are observed between the crystallites and bundles of crystallites. A narrow outermost zone of the layer has a compact structure.

2. The intermediate layer is thin, about one-eighth the shell wall thickness. It is made up of alternate organic and calcified lamellae (Pl. 2, fig. 3). The layer is preserved only partially; in most places it can be recognized as a crack. The outer plate is represented by the acicular-prismatic layer and the coating layer.

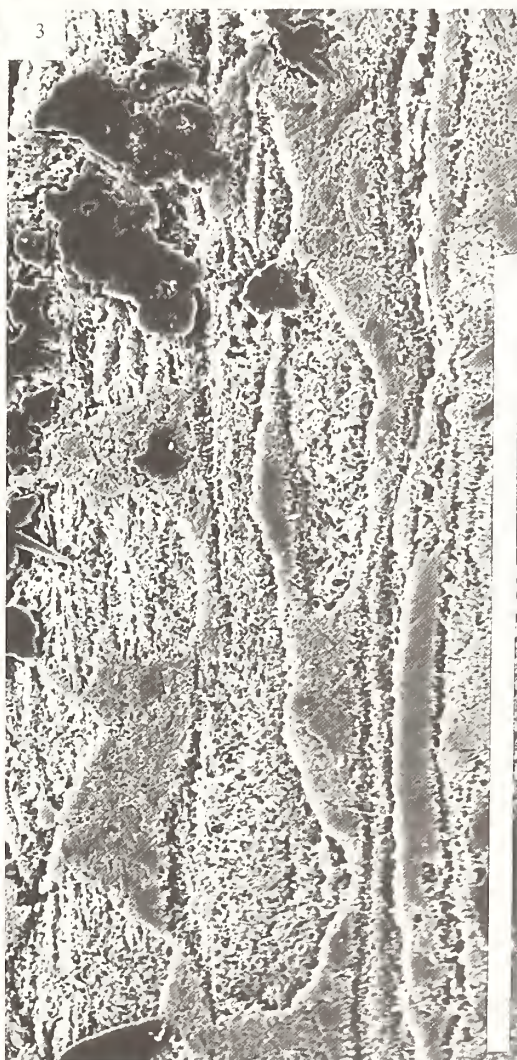
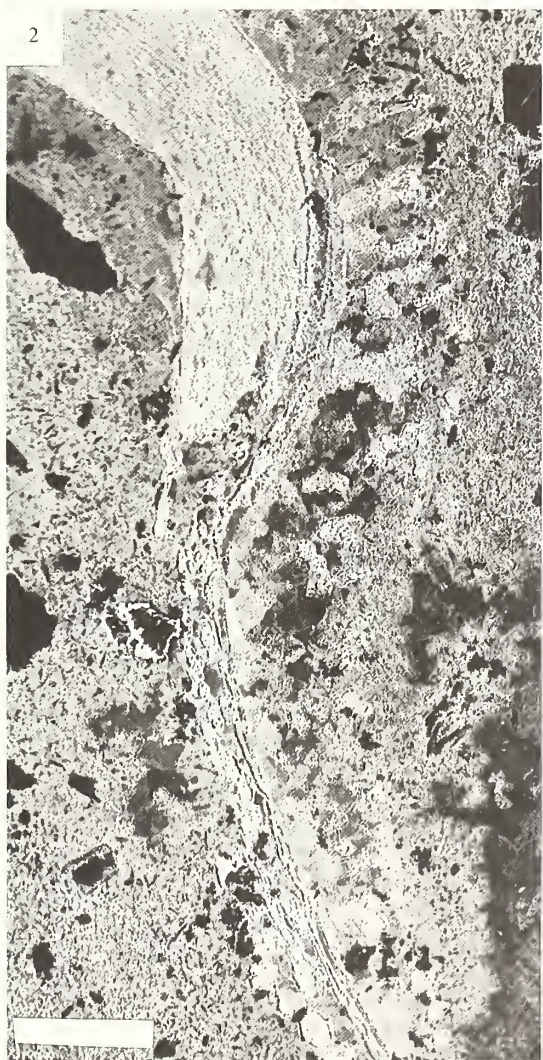
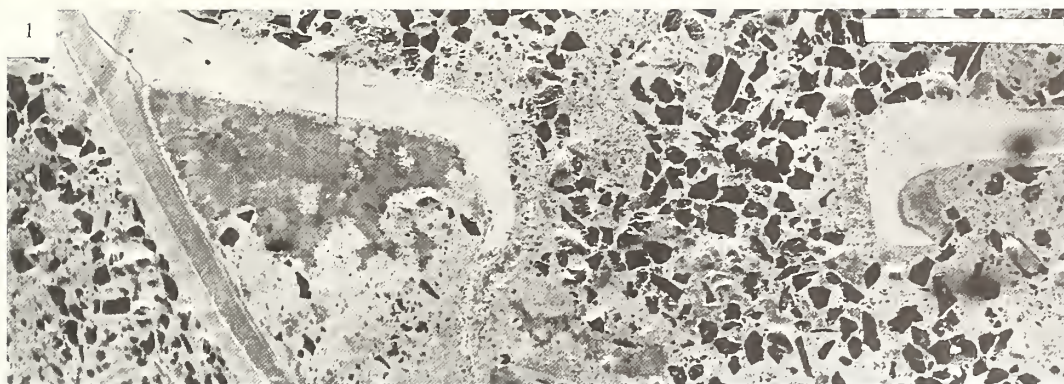
3. The outer principal acicular-prismatic layer comprises about one-third the total thickness of the shell wall (Pl. 2, fig. 1). It shows numerous, closely spaced, distinct, oblique growth lines which have a slightly wavy course and which run at the angle of about 25° towards the aperture (Pl. 3, fig. 1). The layer has a simple prismatic structure consisting of acicular crystallites which are oriented more or less vertically (Pl. 2, fig. 4; Pl. 3, fig. 3).

4. The coating layer is a thin lamellar layer which has a thickness equal to about one-eighth the wall thickness (Pl. 2, figs 1, 4). It seems to consist of alternate uneven organic and calcified lamellae lying parallel to the surface of the wall. Calcified lamellae seem to be composed of irregularly sized prisms, about 5 µm wide, made up of acicular crystallites. The thickness of the lamellae varies between 1 and 2 µm.

Between the inner surface of the shell wall and the septa there is no distinct boundary. At the ultrastructural level, this indistinct boundary is caused by the fact that the lamellae in the septa and in the dendritic prisms of the shell wall are continuous, despite the ultrastructural differences (Pl. 2, fig. 2). An extremely thin, probably organic film lines the adoral septal surface and the shell wall (Pl. 2, fig. 1).

EXPLANATION OF PLATE 5

Figs 1–3. *Adygeya adygensis* gen. et sp. nov.; 3871/127; Upper Aptian; River Hokodz; north-western Caucasus. 1, septal necks with a partly preserved connecting ring; scale bar represents 1 mm. 2, enlarged detail of fig. 1 to show that the connecting ring is composed of two porous, comparatively thick, spherulitic-prismatic layers separated by a thin organic layer; scale bar represents 0.1 mm. 3, enlarged detail of fig. 2 to show the flattened spherulites of the outer layer; scale bar represents 0.1 mm.



DOGUZHAEVA, *Adygeya*

Naefia. The shell wall is characterized by the absence of the nacreous layer (Text-fig. 2A). It is composed of a simple prismatic layer; there are some indications of a thin coating layer (Pl. 6, fig. 3). The shell wall is thin, about the thickness of a septum (Pl. 6, fig. 1). On the ventral side, the inner surface of the shell wall is invested by the long thick mural parts of the septa (Pl. 6, fig. 2). Together they are about three times as thick as the dorsal wall. On the dorsal side, the innermost thin portion of the shell wall covers the anterior ends of the septal mural parts of the septa (Pl. 8, fig. 3). The covering of the mural parts of the last septum is the most prominent (Pl. 9, fig. 1). The boundary between the shell wall and the septa is distinct (Pl. 9, figs 2–3) in contrast to that in *Adygeya*.

The shell/body attachments are visible on the exposed surface of the internal mould of the two phragmocones (Pl. 8, fig. 1; Text-fig. 4C). In each chamber there is a dorsal, unpaired, longitudinal, slender, spindle-shaped scar with width at its maximum near the middle part of a camera, and narrowing towards the posterior and anterior ends (Pl. 8, figs 1–2). The boundary of the scar is distinct along the sides but indistinct near the anterior and posterior ends.

As shown by the SEM micrographs the dorsal scars bear numerous minute pore openings, less than 0.01 mm in diameter (Pl. 8, figs 1–2). Each scar seems to correspond to a dorsal furrow or 'Normallinie' of orthoceroids, bactritoids, belemnoids and aulacocerids, although pores in these furrows are unknown. The pores were previously known in the inner prismatic layer (myostracum) of the Triassic ceratid *Phyllocladiscites*, in the mantle attachment layer at the shell aperture of Recent *Nautilus* (Doguzhaeva and Mutvei 1986a), and in the shell wall of two Lower Cretaceous ammonoids: *Ptychoceras* and *Aconeceras* (Doguzhaeva and Mutvei 1989, 1991). Recently, pores were found on the dorsal furrow of *Mesohibolites* (unpublished data). The occurrence and function of the shell pores in molluscs are still inadequately known; some may strengthen the attachment of the mantle to the shell, notably the pores at the apertural margin of *Nautilus*. In *Naefia* the adhesion between the body and the shell on the dorsal side may have been strengthened by means of the tiny mantle extensions housed inside the pore canals of the dorsal scars.

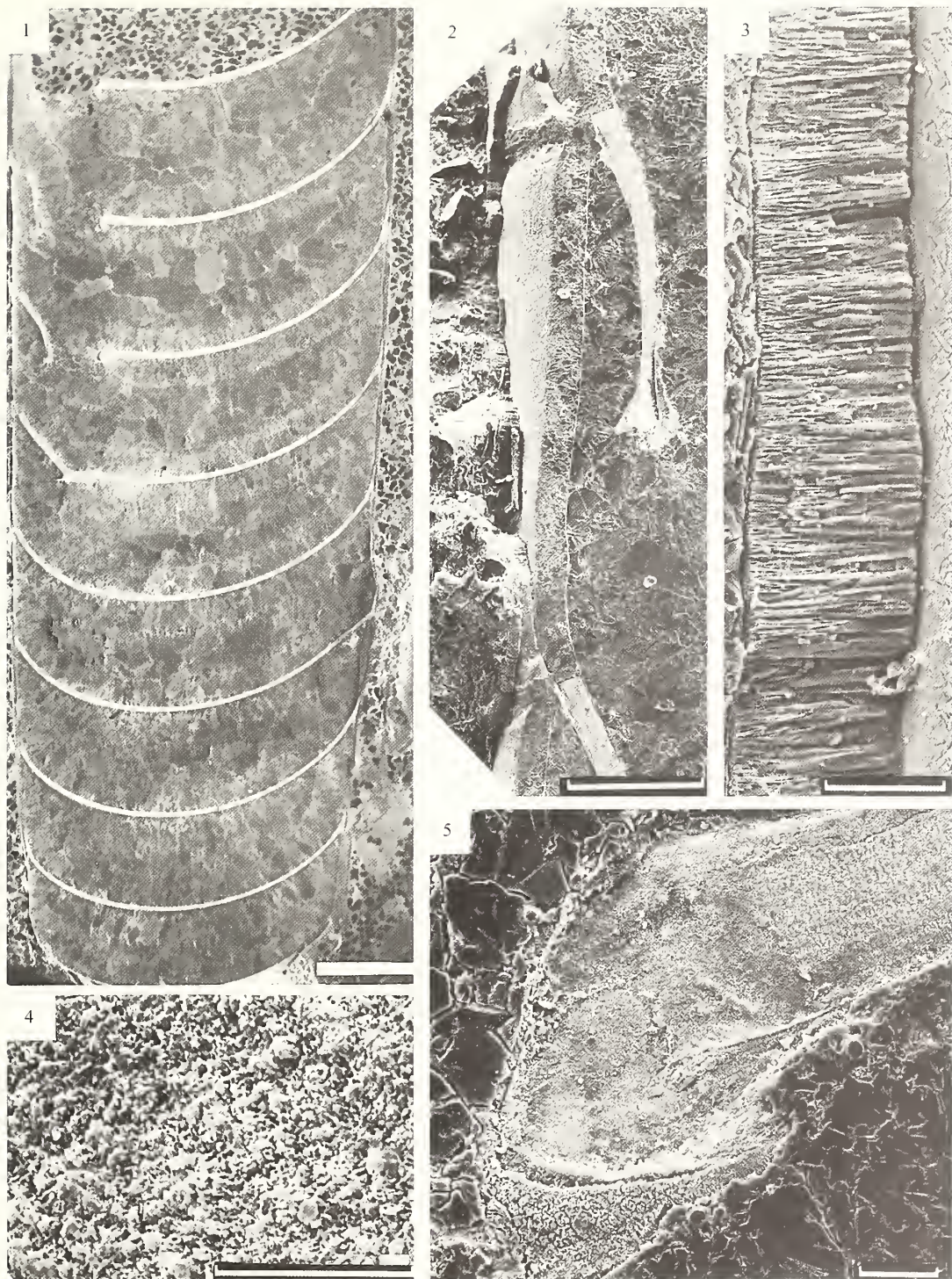
Comparison of the shell wall structure in Adygeya and Spirula

The shell wall in both *Adygeya* and *Spirula* is as thin as the septa and is characterized by the absence of a nacreous layer (Text-figs 1A–B, 3A–C). In both genera it consists of the inner and outer plates separated by the intermediate layer. The inner plate is represented by the inner acicular-prismatic layer with its dendritic structure, which makes up the main part of the shell wall. The intermediate layer is predominantly organic, partly calcified. The outer plate is represented by the outer acicular-prismatic layer, with its simple prismatic structure, and the coating layer with its high content of organic matrix.

The intermediate layer is considered to mark a strong interruption between the secretional zones of the inner and the outer plates. The inner plate seems to have been secreted within the final chamber, whereas the outer plate, on the outer side of the intermediate layer, was formed from the outside of the final chamber. The interruption was probably caused by 'a thick, sharply defined layer of connective tissue (bg.) which extends into the ventral wall of the anterior part of the shell sac', as observed in *Spirula* by Chun (1898–99, p. 335).

EXPLANATION OF PLATE 6

Figs 1–5. *Naefia kabanovi* sp. nov.; 3871/124, holotype; Upper Aptian, River Hokodz, north-western Caucasus. 1, median section of shell, consisting of eight camerae and a short final chamber with preserved apertural margin of shell aperture; scale bar represents 1 mm. 2, detail of fig. 1 showing long mural part of septum and holochroanitic ventral portion of septal neck; scale bar represents 300 μ m. 3, prismatic layer of the shell wall on the ventral side and remnants of a thin lamellar coating layer (left side); scale bar represents 30 μ m. 4, granular appearance of the nacre Type II in septum; scale bar represents 10 μ m. 5, cyrtochroanitic dorsal portion of septal neck with an auxiliary deposit; scale bar represents 30 μ m.



DOGUZHAEVA, *Naefia*

The inner plates in both genera under consideration are very similar, perhaps identical; the outer plates differ in the following features: (1) the acicular-prismatic layer is thick, with oblique growth lines in *Adygeya*, but thin with growth lines parallel to the shell wall surface in *Spirula*; (2) the coating layers are structurally different; the lamellar structure is more prominent in *Adygeya* than in *Spirula*. In addition, the shell surface has a fine reticulate pattern in *Adygeya* but a distinct and coarse reticulate ridge-like pattern in *Spirula*.

The intermediate layer in both genera is predominantly organic; in *Spirula* it shows regular vertical membranes which have not been observed in *Adygeya*.

Comparison of the shell wall structure in Naefia and Spirula, with comments on some other coleoids

The shell wall structures in *Naefia* (Text-fig. 2A) and *Spirula* (Text-fig. 3A–C) are similar in: (1) the absence of the nacreous layer; (2) the predominantly prismatic structure of the shell wall; (3) the comparable thickness of the shell wall to that of the septa; (4) the mode of strengthening of the contact between the shell wall and septa by means of secretion of the flaps, septal ridges and lengthening of the ventral mural parts of the septa; and (5) the presence of the coating layer, which, however, in *Naefia* is lamellar and in *Spirula* acicular-prismatic. Thus, in comparison with that in both *Spirula* and *Adygeya*, the shell wall in *Naefia* was modified by elimination of one of the acicular-prismatic layers.

Among the other coleoids, the Late Campanian–Maastrichtian *Actinosepia* (Waage 1965), Cenozoic *Belosepia*, *Vasseuria*, *Beloptera*, *Belopterina* (Dauphin 1984a, 1984b, 1985a, 1985b, 1986) and Recent *Sepia* (Appellöf 1893; Barskov 1973; Bandel and von Boletzky 1979; Dauphin 1981; Bandel 1989) show some similarity in shell wall (dorsal shield) structure to that in *Adygeya* and *Spirula*. In the genera listed above, the dorsal shield is formed of two calcareous portions separated by an intermediate layer, which is highly variable with regard to its degree of mineralization, but is predominantly organic.

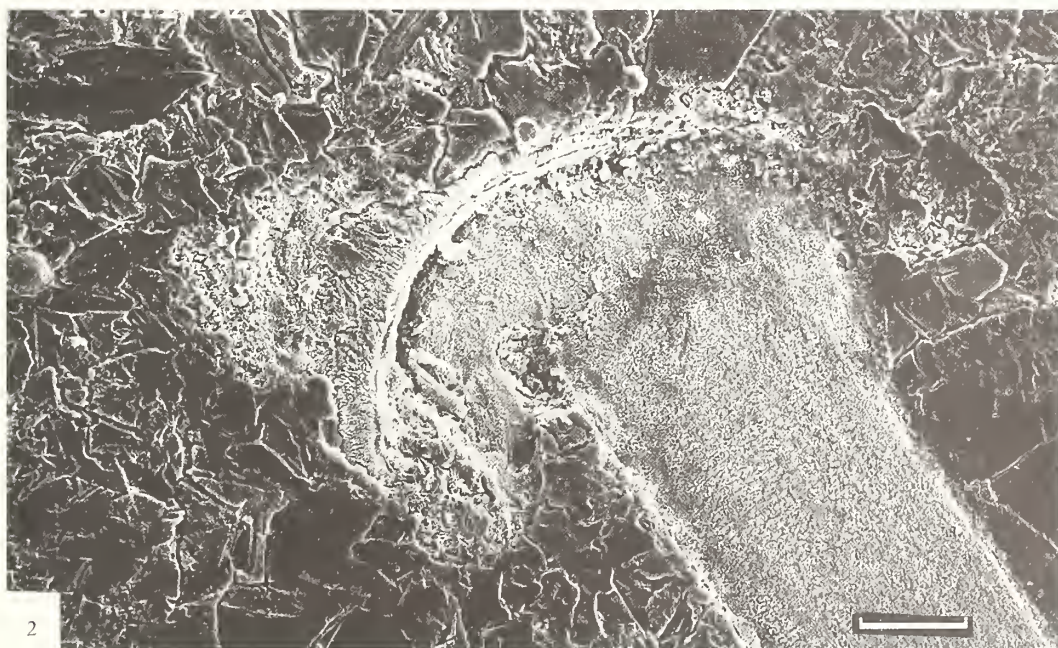
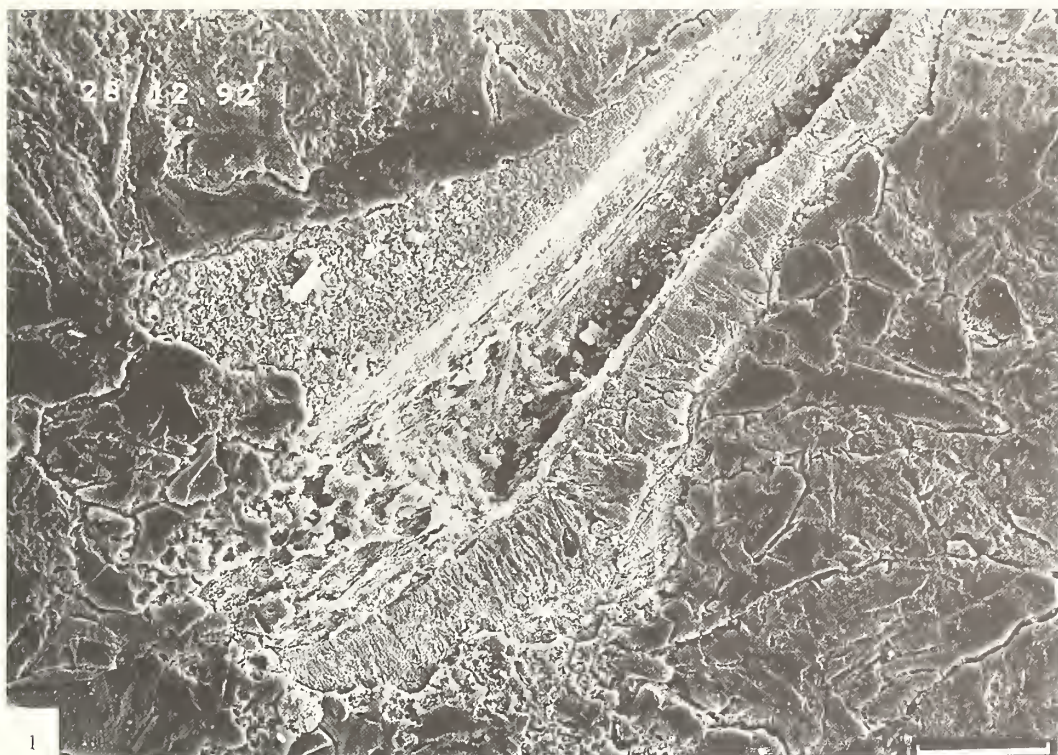
The septa and septal neck structure

Adygeya. Septa are composed of lamello-fibrillar nacre which also forms the septa of *Naefia* and Recent *Spirula*. The adoral septal surface is lined by a thin organic or slightly calcified layer. The mural parts of the septa possess a spherulitic-prismatic structure and, as indicated by their brown colour, seem to contain much organic matrix. Around the siphuncular openings the septa are thicker. The mural parts are thicker than the septa proper. Within the septal necks the organic lamellae are more distinct. The septal structure in *Adygeya* shows great similarity to that in *Groenlandibelus* (Jeletzky 1966; Birkelund and Hansen 1974).

Naefia. The septa and septal necks are formed by lamello-fibrillar nacre. The septal periphery (near the shell wall) possess a nacreous structure with well formed nacreous tablets, but the central part of the septa, as shown by Hewitt *et al.* (1991), has a granular exterior (Pl. 6, figs 4–5; Pl. 7, fig. 2). The adoral surface is covered by an organic sheet (Pl. 9, figs 2–3). Septal necks show distinct organic lamellae, and their distal ends seem to be less calcified (Pl. 7, fig. 1; Pl. 8, fig. 4). The dorsal portions of the last few septal necks show rim-like thickenings directed adorally (Pl. 8, fig. 4; Text-fig. 2C–D),

EXPLANATION OF PLATE 7

Figs 1–2. *Naefia kabanovi* sp. nov.; 3871/124; Upper Aptian, River Hokodz, north-western Caucasus. 1, ventral portion of septal neck lined by thick outer spherulitic-prismatic and thin inner prismatic layer of the connecting ring; the outer surface of the septal neck (left side) is covered by the auxiliary deposit. 2, dorsal portion of the septal neck. Scale bars represent 30 μ m.



similar to the transitional stage to the prochoanitic septal necks in ammonoids (Doguzhaeva and Mutvei 1986b). Similar, rim-like anterior portions of the septal necks were observed in some Early Cretaceous belemnites (Kabanov 1967; unpublished data).

Connecting ring structure

Adygeya. The connecting rings consist of two porous spherulitic-prismatic layers separated by a thin, probably organic layer (Pl. 5, figs 1–3; Text-fig. 1A, C). The outer layer is a structurally modified continuation of the septal neck; it is composed of flattened spherulites with numerous interspaces (Pl. 5, figs 2–3). The inner layer is composed mainly of elongated prisms or bundles of prisms oriented with their long axes perpendicular to the septal neck and separated by numerous interspaces. At the septal necks the inner layer has about the same thickness as the necks but it grows thinner towards the central part of the camera. The intermediate organic layer lines the septal neck (Pl. 5, fig. 2).

Naefia. The connecting rings consist of two layers (Text-fig. 2A–B). The outer layer is thick spherulitic-prismatic in structure. It seems to represent a structurally modified continuation of a septal neck. The inner layer is thin, probably slightly calcified or organic. The auxiliary deposits are well-developed and give a swollen shape to the ends of the septal necks (Pl. 6, fig. 2; Pl. 7, figs 1–2). The siphuncular structure in *Naefia* is similar in all known details to that in *Groenlandibelus* (Jeletzky 1966).

EVOLUTIONARY IMPLICATIONS

The new Aptian species *N. kabanovi* possesses all the general features which occur in the Late Cretaceous *N. neogaia*; the structure of the initial portion of the shell is still unknown in both species. There is high stability in the shell morphology of this genus. Moreover, the siphuncular structures, which were previously unknown in *Naefia*, stress the similarity between *Naefia* and *Groenlandibelus* and confirm the placement of *Naefia* within the Groenlandibelidae, which was questioned by Engeser (1990), and the placement of Groenlandibelidae within the order Spirulida (former Sepiida), which was doubted by Meyer (1993).

The family Adygeyidae, comprising the single Aptian genus *Adygeya*, represents another branch, distinctly different from the Groenlandibelidae. This demonstrates the diversity of Early Cretaceous spirulids. The comparison of the shell wall structure in *Adygeya* and *Spirula* leads to the conclusion that in the lineage of Spirulida the shell possessed an outer plate instead of a rostrum. Therefore, the taxa which had a rostrum can hardly be interpreted as precursors of *Spirula*.

This conclusion contradicts the widespread opinion, introduced by Voltz (1830) and elaborated upon by many, but most significantly by Naef (1921–22), of sepiids (including spirulids) being derived from a belemnoid stock by the reduction and loss of a rostrum (Teichert 1988). It follows from this that forms intermediate between belemnoids and sepiids would be expected to possess remnants of the phragmocones and rostra. Jeletzky did not accept Naef's phylogeny. According to him, 'absence of the primordial guard in Sepiida, combined with retarded appearance of the sepiid sheath, and its asymmetrical mode of the growth do not support the interpretation of the sheath as a gradually dorsalward migrating homologue of the belemnoid guard as attempted by Naef' (Jeletzky 1966, p. 62).

EXPLANATION OF PLATE 8

Figs 1–4. *Naefia kabanovi* sp. nov.; Upper Aptian, River Hokodz, north-western Caucasus. 1, 3871/126; dorsal attachment scar. 2, enlarged detail of Fig. 1 showing numerous tiny pores. 3–4, 3871/125. 3, dorsal mural part of septum, covered by inner portion of shell wall, 4, septal neck, showing adorally directed rim on the dorsal side; inner surface of the septal neck is lined by the connecting ring. Scale bars represent 0.1 mm.



However, Dauphin concluded that the microstructural analyses of the shell 'do not show fundamental differences in the rostral organization of Mesozoic belemnites and Cenozoic sepiids' (Dauphin 1985a, p. 70). She assumed that the lamellar layer of the dorsal shield in sepiids represents a modified nacreous layer of the shell of the phragmocone in aulacocerids and belemnites. This means that sepiids, aulacocerids and belemnites have broadly the same three layers (inner prismatic, nacreous and outer prismatic) as in the shell wall of ectocochleates (Dauphin 1985a).

The caecum and prosiphon observed in *Spirula* and *Groenlandibelus* are expected to be the characteristic features of the whole order Sepiida (Jeletzky 1966). Jeletzky assumed that Sepiida evolved from ancestors possessing orthoconic phragmocones, shallow lobate sutures, and both the caecum and the prosiphon within the protoconch. Recently, the initial portion of the phragmocone showing the caecum and prosiphon were discovered in the Danian sepioid *Ceratisepia* and the Eocene *Belosepia* (Meyer 1993). This confirms the assumptions that both caecum and prosiphon are diagnostic of Sepiida *sensu* Jeletzky. On the other hand, Meyer (1993) did not attach importance to the differences in protoconch structure, but shared Naef's opinion that sepiids derived from forms which were similar to *Conoteuthis*. He assigned Groenlandibelidae to Diplobelina. However, as Jeletzky (1966) convincingly showed, groenlandibelids differ from diplobelins in possessing a caecum and prosiphon.

Thus, the Aptian coleoids *Adygeya adygensis* and *Naefia kabanovi* seem to confirm that Mesozoic precursors of the Tertiary Sepiida and the Late Cretaceous Groenlandibelidae must have been similar to *Groenlandibelus* and *Naefia*. Recent *Spirula* inherited a shell wall structure which is close to that of *Adygeya*, and a siphuncular structure similar to that of *Naefia*. Comparative studies of *Adygeya*, *Naefia* and *Spirula* demonstrate that spirulids possessed a special kind of internal shell which could hardly be derived from that of the belemnites.

The material studied has led to the conclusion that in the superorder Decabranchia of Doyle *et al.* (1994), which includes *Adygeya*, *Naefia*, *Groenlandibelus*, *Actinosepia*, *Spirula*, *Sepia*, *Belosepia*, *Vasseuria*, *Beloptera* and *Belopterina*, the nacreous layer is absent from the shell wall, whereas in the superorder Belemnoida (Doyle *et al.* 1994), including Aulacocerida (Bandel 1985; Dauphin 1985a), Belemnitida (Barskov 1972–73; Dauphin 1985a) and Diplobelida (unpublished data), it is present. Taking into consideration the high stability of the shell wall structure in cephalopods, I suggest that this difference indicates an early divergence of the two superorders.

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EXPLANATION OF PLATE 9

Figs 1–3. *Naefia kabanovi* sp. nov.; 3871/124; Upper Aptian, River Hokodz, north-western Caucasus. 1, apertural margin on the dorsal side of fully grown shell, showing that the main portion of the shell wall formed a flap around the mural part of the last septum; scale bar represents 100 μ m. 2, contact between septum and shell wall; scale bar represents 30 μ m. 3, enlarged detail of fig. 2 to show: (a) nacreous structure of the mural part of a septum with well-developed nacreous tablets; (b) organic membrane on the adoral surface of septum; (c) simple prismatic structure of the shell wall on the dorsal side; (d) nearly equal thickness of the septum and shell wall; and (e) distinct boundary between shell wall and septum; scale bar represents 30 μ m.



DOGUZHAEVA, *Naefia*

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SINISTRAL HYPERSTROPHIC COILING IN A DEVONIAN GASTROPOD FROM BOHEMIA WITH AN *IN SITU* OPERCULUM

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ABSTRACT. A paucispiral operculum is described *in situ* in a specimen of *Tychobrahea aerumnans* from the Devonian of Bohemia. The small turbiniform gastropod shell appears to be dextrally orthostrophically coiled in similar fashion to most other fossil and extant gastropod shells, but the clockwise-coiling of the exterior surface of the operculum indicates that coiling of the shell is sinistral hyperstrophic. This is the first description of an operculate gastropod with this type of coiling in the fossil record.

To most people, a conispiral shell is the characteristic feature of gastropod molluscs, although this type of coiling into a three-dimensional spire is neither restricted to the class nor diagnostic of it. Rather, gastropods are distinguished by having undergone torsion at some stage in their developmental or evolutionary history, a process involving rotation of the originally posterior mantle cavity to an anterior position. The gut and visceral loop become twisted and the anatomy of the gastropod is profoundly asymmetrical (Cox 1960). Torsion is anti-clockwise in the vast majority of living gastropods and the paired organs associated with the originally posterior mantle cavity are reduced or lost in most gastropods on the post-torsional right side, when viewed from above. Such a gastropod can be described as anatomically dextral; anatomical sinistrality involves clockwise torsion and reduction of organs on the post-torsional left side (Robertson 1993).

Torsion and the resultant asymmetry of the soft parts have been considered to be closely related to the conispiral coiling of most gastropod shells (cf. Knight 1952; Pojeta and Runnegar 1976; Linsley 1978a; Lever 1979; Robertson 1993). Conispiral coiling, however, is also developed in untorted molluscs such as the onychochilid paragastropods (Linsley and Kier 1984) and the Pelagiellidae (cf. Peel 1992). On the other hand, many limpet gastropods show a high degree of bilateral symmetry in the adult shell while the soft parts are conspicuously asymmetrical (Fretter and Graham 1994). Changes in the form and orientation of conispiral shells are closely linked to anatomical adaptation and evolution of the gastropod animal. Re-orientation of the shell and associated morphological change are two of the most conspicuous trends in gastropod evolution (Linsley 1978a, 1978b).

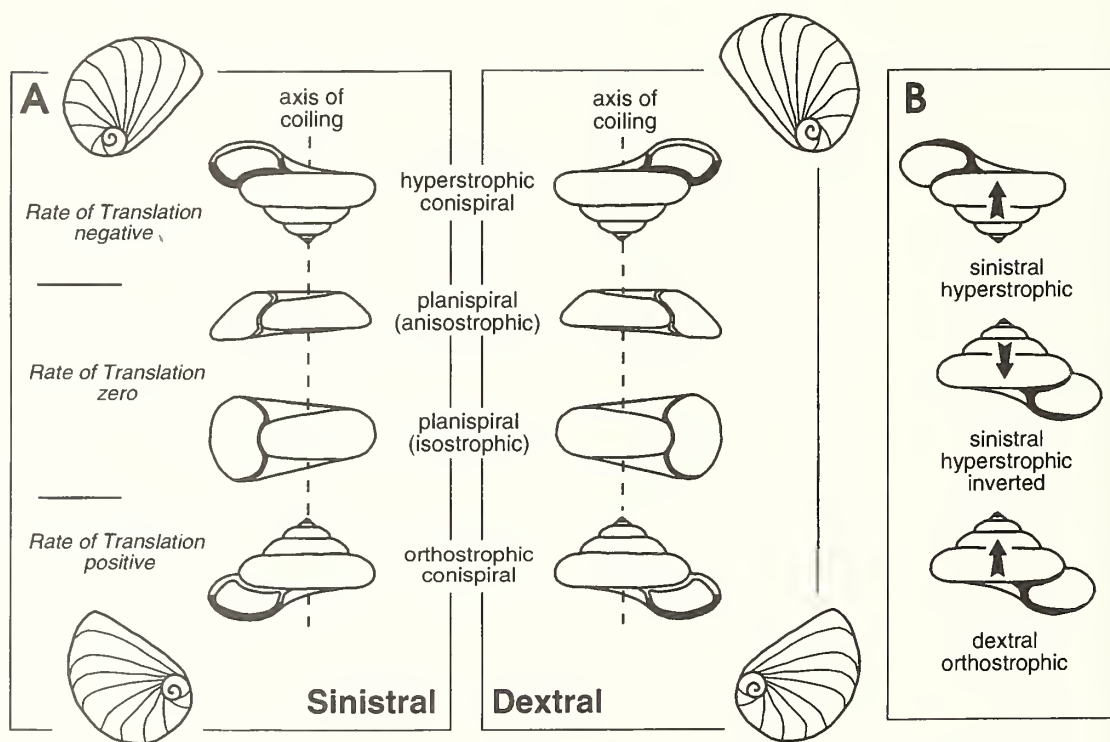
The terms dextral and sinistral are most commonly applied to the direction of coiling of gastropod shells. Most gastropod shells are coiled dextrally when viewed in standard orientation, i.e. the aperture lies to the right of the axis of coiling when the shell is placed with the aperture facing the viewer, with the apex uppermost and the axis of coiling vertical (Text-fig. 1). In apical view, such a shell increases in a clockwise direction with the addition of successive increments of growth. A mirror image of a dextral shell produces a form in which the aperture lies to the left of the axis in apertural view, and this sinistral shell increases in an anti-clockwise spire when viewed apically.

Sinistral coiling is much less common than dextral coiling within the Gastropoda but it is widespread, particularly within pulmonates (Vermeij 1975, 1993; Robertson 1993). Sinistral species or genera, such as the familiar *Neptunea contraria* or *Sinistrofulgur sinistrum*, occur in many groups and at least one marine family with an extensive fossil record, the Amberleyidae, contains a conspicuous number of sinistral forms (cf. Knight *et al.* 1960; Vermeij 1993). Sinistral individuals

sometimes occur as rare mutations within otherwise dextral populations (cf. Gould 1993, p. 452; Robertson 1993, figs 14–17).

Sinistral and dextral shells need not be conspiral. If the rate of translation (parameter T of Raup 1966) of the whorl along the axis of coiling with growth is zero, the resultant shell form is planispiral with coiling within a single plane. Most planispiral gastropod shells are conspicuously anisotropic, enabling easy recognition of the type of coiling. If the shell is isotropic, however, and bilaterally symmetrical about a plane perpendicular to the axis of coiling, the form of the shell alone offers no clue concerning the direction of coiling. Isotropic coiling is characteristic of bellerophonitoidean gastropods which were prominent in the Palaeozoic.

If the rate of translation (T) of the whorl is negative the shell can be considered to grow up its axis of coiling relative to the normal condition where T is positive and the shell grows down the axis. Such shells with negative translation are termed hyperstrophic while positive translation produces orthostrophic coiling (Text-fig. 1A). In a hyperstrophic shell, the whorls are extended into a basal



TEXT-FIG. 1. A, coiling patterns in gastropod shells comparing orthostrophic and hyperstrophic coiling in sinistral and dextral morphologies, together with schematic illustrations of associated opercula (viewed from the exterior). Equivalent areas of the shell aperture in orthostrophic and hyperstrophic conspiral shells are coloured black, B, identity in shell form between sinistral hyperstrophic coiling and the dextral orthostrophic coiling which is overwhelmingly dominant within the Gastropoda. These two morphologies can only be separated by study of soft anatomy or by comparing the coiling directions of the shells with their respective opercula. Arrows indicate 'up' in standard orientation.

spire equivalent to the lower surface (base) of the orthostrophic shell in standard orientation, and not to the extended orthostrophic spire. Dextral and sinistral morphologies are geometrically possible within both orthostrophic and hyperstrophic shells. Dextral and sinistral morphotypes are essentially mirror images of each other, also in terms of anatomy, but no similar relationship exists

between the orthostrophic and hyperstrophic forms (Text-fig. 1b). Anatomical dextrality is present in gastropods with dextral orthostrophic and dextral hyperstrophic shells, the latter case giving rise to the description of anatomically dextral gastropods in apparently sinistral shells.

Comparison of the shell morphologies illustrated in Text-figure 1 reveals a conchological dilemma, for it is evident that a dextral orthostrophic shell may be morphologically indistinguishable from a sinistral hyperstrophic shell (and a sinistral orthostrophic from a dextral hyperstrophic) even though equivalent areas of the whorl profile are located at different locations within the shell viewed as a whole. In the living gastropod the issue can be resolved by reference to soft anatomy but this approach fails in the fossil record. Analysis of shell features such as apertural shape may provide useful clues in unusual morphologies (cf. Linsley and Kier 1984) but the student of fossil gastropods will usually describe a shell in terms of orthostrophic coiling, mainly on the basis of the knowledge that hyperstrophic coiling is very rare at the present day (Robertson 1993).

One shell feature capable of preservation in the fossil record provides irrefutable evidence concerning direction of coiling, namely the direction of coiling of the spiral operculum (there are also opercula which grow by concentric growth (cf. Yochelson 1990; Gubanov and Yochelson 1994). When viewed externally, spiral gastropod opercula coil in the opposite direction to the direction of coiling of the shell, as a function of the addition of consecutive growth increments of the operculum at the parietal margin of the aperture (Hickman and McLean 1990). Thus, the outer surface of the operculum is coiled sinistrally (anti-clockwise) in a dextrally coiled orthostrophic shell but dextrally (clockwise) in a sinistrally coiled orthostrophic form (Text-fig. 1). The operculum is also sinistral in a dextral hyperstrophic shell viewed in the correct orientation, with the basal spire down. If the shell is incorrectly interpreted as sinistral orthostrophic, however, and oriented with the basal spire pointing up, the operculum will be coiled in the same direction as the shell.

Most living shell-bearing gastropods possess an operculum at some stage in their development. Isolated opercula (Pl. 1, fig. 1) are well known as fossils within the Palaeozoic but are usually uncommon (Yochelson 1979). Records of fossil gastropod shells with the operculum preserved *in situ* within the shell aperture are few (e.g. Perner 1903, 1907, 1911; Teller 1910; Knight 1941; Boucot *et al.* 1966; Yochelson and Linsley 1972; Yochelson and Wise, 1972; Linsley 1978c; Yochelson 1990; Gubanov and Yochelson 1994). Lindström (1884, pl. 17; see also Peel 1984) illustrated opercula *in situ* in *Oriostoma cornuta* and *O. globosa* and a variety of isolated opercula from the Silurian of Gotland, Sweden. Several of the described associations of operculum and shell have enabled important re-interpretation of the nature of coiling of the host shell. Thus, the widespread and abundant Ordovician *Machyrites* is interpreted as dextral hyperstrophically coiled rather than sinistral orthostrophic on the basis of its operculum (Knight *et al.* 1960; Rohr 1979; Yochelson 1979), although Yochelson (1990) reviewed this interpretation of the operculum. Similarly, Linsley (1978c) demonstrated that Devonian omphalocirrids were dextral rather than sinistral on the basis of finds of *in situ* opercula.

In the present paper we describe a unique specimen of the gastropod *Tychobrahea aerumnans* Horný, 1992 from the Devonian of Bohemia in which the operculum is preserved essentially *in situ* within the aperture. This specimen is of particular interest in that the direction of coiling of the operculum demonstrates that the Bohemian gastropod was sinistral hyperstrophic rather than dextral orthostrophic, as cursory examination of the conispiral shell might suggest. This is the first report of this exceptional type of coiling in marine gastropods in the fossil record. Sinistral hyperstrophic occurs in many planorboid gastropods but these freshwater pulmonates lack an operculum, and characteristically have an almost planispiral shell.

SYSTEMATIC PALAEONTOLOGY

Tychobrahea aerumnans Horný, 1992

Plate 1, figures 2–5, 8

1992 *Tychobrahea aerumnans* Horný, p. 104, pl. 3, figs 1–4.

Description. Only one specimen with the operculum preserved *in situ*, but slightly displaced, has been found among many hundreds of isolated specimens of this species collected from various Lower Devonian micritic limestones in the vicinity of Prague. Horný (1992) designated this specimen as the holotype of *Tychobrahea aerumnans*. It is an almost complete shell, isolated from weathered and washed limestone, and it is preserved as recrystallized calcite. It was collected by the late F. Hanuš from the 'Red Quarry' near Klukovice, Prague, in the Pragian (Lower Devonian) Dvorce-Prokop Limestone.

The holopeiform shell is regularly coiled, originally with weak prosocline growth lines. The whorls are slightly shouldered but the angulation is not reflected on the internal shell surface. The base is rounded, anomphalous, with the umbilical region partly filled with a thick, crescent-like, flattened columellar callus. The shell wall forming the apertural margin slopes adapically in towards the shell interior with shallow convexity from the acute outer margin; the internal profile of the aperture is almost circular. The shell is thick, thinnest in the parietal region.

The operculum is preserved within the entrance of the last whorl; it has been pressed in obliquely and slightly rotated after death. On account of this oblique orientation, it is possible to observe both the external surface and the lateral profile of the operculum. The inner surface of the operculum has been cemented to the internal shell wall and partly covered by the shell of a tentaculite. The outer surface of the operculum is more intensely weathered than the shell with corrosion mainly following the opercular sutures, an observation also made by Yochelson and Linsley (1972) in *Cyclonema lilydalense* from the lowermost Devonian of Australia.

The operculum is almost circular, relatively massive and thick (about 0.35 mm at the periphery, compared with the thickness of the shell itself, 0.25 mm, at the aperture below the periphery; the total height of shell is 6.8 mm). The operculum is completely recrystallized, translucent, with no traces of growth increments. In profile, the edge of the operculum is concave, sloping in towards the shell interior such that the diameter of the outer surface of the operculum is larger than the diameter of the inner surface. This lateral margin of the operculum corresponds in shape to the bevelled edge of the aperture, although the operculum in the available specimen is withdrawn slightly into the aperture. The outer surface clearly demonstrates that the operculum is paucispiral, regularly and slowly expanding in a clockwise direction (Pl. 1, fig. 2). The rate of rotation corresponds approximately to the growing rate of the shell; the angle of accretion is high, approximately 90 degrees. The outer surface of the operculum is generally flat but, as mentioned above, corrosion has emphasized the opercular sutures. The latest preserved volution is slightly concave medially but the coarse preservation obscures the nature of the earliest growth stages. The internal surface of the operculum is not visible.

Some doubt exists concerning the position of the accreting zone of the operculum relative to the shell. At the present time, the accreting margin faces the columellar lip. The internal profile of the aperture is circular, however, making it difficult to restore the operculum to its original position.

Occurrence and associated fauna. *Tychobrahea aerumnans* is one of the most abundant gastropods within the Lower Devonian of Bohemia (Horný 1992). These morphologically variable, thick-shelled gastropods, possible sedentary suspension feeders, were seemingly quite successful in the low energy conditions prevalent during the Early Devonian and represented by micritic limestone facies. *T. aerumnans* is totally absent from the

EXPLANATION OF PLATE I

Fig. 1. External view of an isolated paucispiral operculum, probably of *Australonema* cf. *guillieri* (Oehlert), from the Lower Devonian (Pragian), Koněprusy Limestone, Koněprusy, Bohemia (after Horný 1994); National Museum, Prague, L 8764; the operculum is coiled in an anti-clockwise spiral, indicating that the host gastropod shell was dextral orthostrophic; $\times 8$.

Figs 2–5, 8. *Tychobrahea aerumnans* Horný, 1992, Lower Devonian (Pragian), Dvorce-Prokop Limestone, Praha-Klukovice, Bohemia; National Museum, Prague, L 29194; holotype. 2. oblique view of the aperture and the upper surface showing the clockwise coiling of the outer surface of the operculum; $\times 15$. 3–5, three different apertural views oriented as a sinistral hyperstrophic gastropod with the operculum *in situ*. Note that the operculum is slightly displaced so that its concave lateral margin is visible in 5; $\times 11$. 8, the same specimen in apertural view, but oriented as a dextral orthostrophic gastropod; $\times 11$.

Figs 6–7. *Tychobrahea* aff. *T. aerumnans* Horný, 1992; lateral and oblique apertural views showing a prominent callus in the umbilical region; Lower Devonian (Dalejan), Třebotov Limestone, Praha-Holyně, Bohemia; National Museum, Prague, L 29233; $\times 11$.



1



2



3



4



5



6



7



8

Koněprusy bioherm and its surroundings. In contrast with other contemporaneous gastropods within the low energy environments, such as *Hanusispira*, *Palaeozygopleura* and *Diplozone*, *T. aerumnans* is extremely variable. According to Horný (1992), this variability is mainly expressed in the height of the shell, presence or absence of an umbilicus, the profile of the upper part of the whorl (whether gradate or rounded) and the degree of development of the columellar callus. Other co-occurring gastropods, especially the loxonemataceans and pleuromariaceans, frequently show evidence of shell repair, but repaired injuries have not been observed in *T. aerumnans*.

Associated gastropods include *Tropidodiscus*, *Kodymites*, *Paleuphemites*, *Trochoclisa*, *Straparollus*, *Ptychomphalina*, *Hanusispira*, *Pragoloron*, *Umbotropis*, *Vladanella*, *Dongiovannia*, *Oriostoma*, *Naticopsis*, *Diplozone*, *Loxonema*, *Katoptychia*, *Palaeozygopleura* and subulitids, all associated with a diverse invertebrate fauna. The low energy environment was dominated by deposition of soft calcareous mud, microbioclastic material (mainly crinoidal) and diffuse organic matter. A unifying theme within the whole fossil assemblage is small size (with the exception of local accumulations of large trilobite carapaces). Noteworthy, is the rare occurrence of dwarfed specimens of gastropods, such as *Platyceras* (*Praenatica*), which reach their normal size in the reef facies some 30 km to the west. All washed samples contain a high percentage of undamaged juvenile gastropod shells, together with tiny remains of echinoderms, holothuroid plates and foraminifers, but isolated gastropod opercula are lacking.

THE QUESTION OF HYPERSTROPHY

It is a character of spiral gastropod opercula, when viewed externally, that they are coiled in the opposite direction to the coiling of the shell (Cox 1960; Yochelson and Linsley 1972; Linsley and Kier 1984; Robertson 1993). Thus, as noted above, in a typical dextral orthostrophic gastropod viewed from the apex, coiling is clockwise and the operculum is coiled anti-clockwise when viewed from the exterior (Pl. 1, fig. 1). When viewed from the internal surface, the coiling of the same operculum is clockwise.

The operculum in *Tychobraea aerumnans* is coiled clockwise on the outer side as preserved (Pl. 1, fig. 2) which indicates that the shell is coiled anti-clockwise, i.e. sinistrally. Clearly, the shell appears to be dextral (with the aperture at the right) when viewed in standard orientation (Pl. 1, fig. 8) whereas the aperture would lie to the left in a sinistral form. This apparent incongruity is resolved by interpreting the shell of *T. aerumnans* as hyperstrophic. Oriented as a sinistral hyperstrophic gastropod and viewed from the upper umbilical surface (Pl. 1, fig. 2), *T. aerumnans* is coiled anti-clockwise while the operculum is coiled clockwise, satisfying the relationship between shell and operculum noted above. A similar argument has been presented by Linsley (1978c) in his interpretation of the orientation of omphalocirrid shells, although in this case he demonstrated that shells widely presumed to be sinistral were dextral, on the basis of their operculum.

This is the first description of a fossil marine gastropod interpreted as sinistral hyperstrophic and the only described example of an operculum in such a shell form. On account of our assertion, and the rarity of hyperstrophic gastropods at the present day (cf. Linsley and Kier 1984; Robertson 1993; Vermeij 1975, 1993), it is prudent to scrutinize the claim closely.

Our interpretation assumes that the relationship between coiling in the gastropod shell and in the operculum is constant. This relationship was questioned by Rohr and Boucot (1985) while describing isolated opercula from the Lower Silurian of Quebec. They described anti-clockwise coiling on both the inner and outer surfaces of *Oriostoma* opercula when viewed from the respective surface, an observation which requires the inner and outer surfaces to grow in opposite directions. Coiling on the outer surface of the opercula, however, is multispiral while that on the inner surface is paucispiral. Rohr and Boucot (1985) proposed that the anomalous coiling on the interior surface was an artefact possibly resulting from a migrating muscle. Similar opercula illustrated by Lindström (1884) from the Silurian of Gotland appear to support this interpretation and there is little reason to doubt that the familiar association of anti-clockwise opercula (when viewed externally) and a dextral orthostrophic shell is correct (cf. Lindström 1884; Peel 1984).

Incidentally, Gubanov and Yochelson (1994) cited Rohr and Boucot (1985) in interpreting an association of a gastropod and operculum described by Teller (1910) from the Silurian of Wisconsin under the name *Murchisonia conradi*. Similar opercula from the same horizon and general locality

were illustrated by Peel (1987, fig. 14.30c). Teller's (1910, pl. 150, fig. 1) illustration indicates an external mould of the gastropod and an operculum which, as preserved, is coiled in a clockwise direction. Teller (1910) considered the illustration to represent an impression of the outer surface of the operculum. Thus, the operculum itself would be coiled in an anti-clockwise direction when viewed externally. This would indicate a dextral shell which seems to agree with Teller's (1910) illustration, where the apparent sinistrality of the dextral shell results from its orientation with the aperture facing away from the observer. Gubanov and Yochelson (1994) considered Teller's fossil to represent an imprint of the paucispiral inner surface of a multispiral operculum of *Oriostoma*-type such as described by Rohr and Boucot (1985) but the location of the operculum relative to the gastropod shell in Teller's (1910) illustration would imply that *M. conradi* is truly sinistral if this interpretation is correct. This does not appear to be the case but this enigmatic association requires re-description.

The resemblance between illustrations of Teller's (1910) operculum and the operculum of *T. aerumnans* is striking. Notwithstanding the conflicting interpretations, the Wisconsin specimens are undoubtedly external moulds and coiling would be in the opposite direction in the operculum itself, opposite also to that in *T. aerumnans*.

If the presumed outer surface of the operculum in *T. aerumnans* was in fact an internal surface, and the operculum had been post mortally overturned such that the visible outer surface was the true inner surface, it would be possible to interpret *T. aerumnans* as a 'normal' dextral orthostrophic gastropod. Lindström (1884, p. 176) reported an operculum which he interpreted as overturned in a Silurian gastropod from Gotland but provided no illustration. This interpretation of *T. aerumnans* is countered by examination of the lateral margins of the operculum; these clearly slope inwards, with the currently visible outer surface being wider than the inner surface (Pl. 1, fig. 5). In addition, the lateral margins of the operculum are concave, producing a truncated conical form consistent with the function of the operculum as a lid to the shell aperture (cf. Linsley 1978c, pl. 10, figs 13, 16). Isolated Silurian opercula illustrated by Lindström (1884, pl. 17) are also conical, but the convex sides and the beehive form of the external surface show no similarity to the operculum of *Tychobrahea*. Thus, it is unlikely that the presumed outer surface of the operculum of *T. aerumnans* has been incorrectly identified.

The operculum in *T. aerumnans* appears to be smaller than the outer margin of the aperture (as preserved, it is withdrawn within the margin of the aperture; see Pl. 1, figs 2–5). This is a common feature of opercula in living gastropods (cf. Hickman and McLean 1990, fig. 1) and the operculum functions equally well as a protective lid if withdrawn from the outermost margin of the aperture. Deep placing of the operculum also provides added protection against predators which break back the apertural margins as a means of gaining access to the soft parts. It also allows the operculum to be opened slightly for respiration without extension beyond the protective apertural margins.

We cannot fully discount the possibility that an isolated operculum has been placed by chance within the aperture of another gastropod which fortuitously has the same apertural shape and general size as that from which the operculum was originally derived. Such cruel irony would permit the interpretation that the operculum is derived from a sinistral orthostrophic gastropod or a sinistral hyperstrophic gastropod and that it has subsequently been placed within the aperture of a dextral gastropod; the idea is rejected.

Linsley and Kier (1984) proposed a class Paragastropoda to include a number of apparently sinistral untorted molluscs which otherwise have been interpreted as hyperstrophic gastropods (Knight *et al.* 1960). A variety of forms – pelagiellids, onychochilids, macluritids and euomphalids(?) – were included within the class, although the authors accepted that their concept of Paragastropoda was a grade of organization rather than a single clade. A discussion of the scope of the class lies outside the present context but their proposal is relevant since some of the more familiar operculum-bearing gastropods of other authors, e.g. *Maclurites*, *Palliseria*, *Teichispira*, *Omphalotrochus*, were included within the Paragastropoda. Linsley and Kier (1984) interpreted the relative orientation of gastropod and shell in the same way as if these supposed paragastropod molluscs were true gastropods.

Yochelson (1990) pointed out that the operculum in *Machurites* grew by accretion around the entire margin and not just at a narrow growth zone, as is the case with spiral opercula (cf. Hickman and McLean 1990). Such a relationship is also evident in opercula of *Ceratopea* which are locally abundant in the Lower Ordovician of Laurentia (Yochelson 1979). The continuous spiral rotation of paucispiral and multispiral opercula with growth and the deposition of sequential growth increments at the parietal wall require that the interior of the aperture is almost circular in cross section, as in *T. aerumnans* (see also *Liomphalus northi* as illustrated by Yochelson and Linsley 1972, pl. 2, figs 1–5; Linsley 1978c, pl. 10, figs 13, 16; Peel 1987, fig. 14.30A). The angulation on the shell exterior in *T. aerumnans* is of no consequence, as it is not reflected on the shell interior. Spiral growth of a tightly fitted operculum with this degree of spiral rotation is not possible within the polygonal aperture of *Machurites* and *Ceratopea* and growth occurs around the entire margin of the operculum, but not equally. Opercula of *Machurites* and *Ceratopea* are still coiled, however, due to the differential growth at the opercular margin. This anti-clockwise curvature of the exterior surface of the operculum in *Machurites* supports interpretation of the shell as dextral hyperstrophic, although strong evidence for this interpretation also lies in functional morphological interpretation of the shell alone. *Machurites* undoubtedly followed a sedentary existence with its flattened lower surface in direct contact with the substrate; the hyperstrophic coiling of the shell reflects the influence of the surface upon which the probably filter feeding gastropod lived.

Onychochilid paragastropods are commonly more relatively high spired than most of the generally low spired operculum-bearing forms mentioned above but they show a range of shell morphologies quite unlike that seen in *T. aerumnans*. Onychochilid opercula are not known, although Linsley and Kier (1984) expected that they existed. We find little reason to interpret *T. aerumnans* as an onychochilid paragastropod despite our suggestion that it is hyperstrophically coiled. Moreover, sinistral hyperstrophy is not a known feature of paragastropods or gastropods, with the exception of the low spired planorboids. Indeed, without evidence from the operculum, the condition is hardly recognizable in fossil material.

At the present day sinistral hyperstrophy is known only within the freshwater pulmonate Planorbioidea which lack an operculum and display anatomical sinistrality in an almost planispiral, slightly hyperstrophic shell (Robertson 1993). The most familiar example is perhaps *Carinifex newberryi* from western North America (cf. Robertson 1993, fig. 21) but planorboids have a geological record extending back to the Jurassic (Tracey *et al.* 1993). Hyperstrophic coiling also occurs in the larval stages of shelled opisthobranchs, most architectonicid prosobranchs and in some freshwater snails (Robertson 1993) but adults revert to orthostrophy. *Lanistes* retains dextral hyperstrophy into adulthood.

Recognition of the sinistral hyperstrophic form of *T. aerumnans* complicates interpretation of its systematic position. It is not possible to decide if the coiling pattern is typical of the species or genus alone, or whether it is a character of a higher taxon. It is also possible that the single specimen with the operculum in place is sinistral hyperstrophic and most other individuals were dextral orthostrophic. By comparison, in the family Ampullariidae, some genera are dextral conspiral, others are planispiral while the genus *Lanistes* is hyperstrophic (Cox 1960). The shell of *T. aerumnans* itself shows some similarity to members of the family Holopeidae, but typical representatives of this family are thin-shelled and without a columellar callus. Holopeids are apparently mainly dextral but the Devonian *Antitrochus* is sinistral.

The strong flattened crescentic callus of *T. aerumnans* invites comparison with some genera of the family Anomalidae but apertural characters are dissimilar. Moreover, the multispiral operculum of *Turbiniopsis* confirms its orthostrophic character (Tyler 1965).

A third possibility for comparison is found with members of the superfamily Euomphaloidea, traditionally regarded as gastropods but tentatively interpreted as paragastropods by Linsley and Kier (1984). The variability of shell morphology seen in *T. aerumnans* is also present in *Straparollus*, and the whorl profile in many euomphaloids is also a point of similarity. On the other hand, the multispiral operculum of omphalocirrids and the similar opercula of oriostomatids do not compare well with the paucispiral operculum of *T. aerumnans*. However, the great diversity of opercular form

within the trochacean gastropods recorded by Hickman and McLean (1990) casts doubt upon the utility of this character in gastropod classification.

Horný (1992) placed *Tychobrahea* within a new family, Tychobraheidae, together with *Komenskyspira* and *Asinomphalus*. Unfortunately, opercula are not known in these two genera. Other possible candidate family members include *Micromphalus*, *Straparollina* and some genera currently classified within the Anomphalidae, although opercula are not known in these taxa. It is likely that some species assigned in the literature to the genera *Straparollus* and *Holopea* are also tychobraheids.

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TWO *OSMUNDOPSIS* SPECIES AND THEIR STERILE FOLIAGE FROM THE MIDDLE JURASSIC OF YORKSHIRE

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ABSTRACT. *Osmundopsis hillii* sp. nov., from Hasty Bank, Yorkshire, is probably the fertile foliage of *Cladophlebis harrisi*. New material of *Osmundopsis sturii* from Gristhorpe suggests that it might be the fertile foliage of part of *Cladophlebis denticulata*. Sterile foliage that was provisionally assigned to *O. sturii* is probably a large form of *Eboracia lobifolia*.

HARRIS (1931) established the genus *Osmundopsis* for fertile osmundaceous remains in which no lamina is present in the pinnules, and the sporangia are arranged in clusters as in the extant genus *Osmunda*. The type species is *Osmundopsis sturii* (Raciborski) Harris (basionym *Osmunda sturii* Raciborski, 1890) known from the Upper Liassic of Poland (Raciborski 1890; Harris 1977) and Iran (Schweitzer *et al.* in press), and the Middle Jurassic of Yorkshire (Harris 1961, 1977), Abchasia (Krystofovich and Prynada 1933) and China (Duan 1987). Several other species have been found in Mesozoic strata including the well-known *O. plectrophora* from the Liassic of Greenland (Harris 1931).

Over several years, Dr C. R. Hill (London, UK) collected fertile *Osmundopsis* material at Hasty Bank, Yorkshire. He prepared the material, made photographs and isolated some spores from one of the specimens (the slide with these spores was damaged beyond repair in the mail when the present author, who studied these spores, returned it to him). This *Osmundopsis* material (including some newly isolated spores) is described here as a new species which I name after Dr Hill in honour of the work he did on the Yorkshire Jurassic flora, especially that of Hasty Bank. *Cladophlebis harrisi* van Cittert, 1966 is very probably the sterile foliage belonging to *Osmundopsis hillii*.

Dr J. Lovis (formerly Leeds, UK, now Christchurch, New Zealand) had a large collection of Yorkshire Jurassic material which he presented to The Natural History Museum, London on leaving England. This collection includes several specimens of *Osmundopsis sturii* which extend our knowledge of this species. A new specimen of *O. sturii* in the Utrecht collection (the Netherlands) is also included in the description. The study also includes sterile foliage that Lovis thought might belong to *O. sturii*. Although it was first thought to be a new species, it proved to be merely a large form of *Eboracia lobifolia* (Dicksoniaceae). Some of the smaller specimens of this sterile material showed all the features characteristic of *E. lobifolia* (including the typical forked basal pinnule) and transitional specimens are also present. The sterile foliage belonging to *O. sturii* is still a problem, but might well be a small form of *Cladophlebis denticulata*.

MATERIAL AND METHODS

The material of *Osmundopsis hillii* was collected by Dr C. R. Hill at Hasty Bank, Yorkshire [NZ 568035], especially from the claystone layer in the lower part of the plant bed (see Hill and van Konijnenburg-van Cittert 1973). This plant bed is in the Saltwick Formation (Aalenian). Most of the *Osmundopsis sturii* material was collected by Dr J. Lovis from the main Gristhorpe plant bed at Cayton Bay (near Scarborough; TA 083842), where the Utrecht specimen was also found. One

specimen was found at the Cloughton Wyke *Solenites*-bed [TA 020951]. Both these localities belong to the Cloughton Formation, Gristhorpe Member (Lower Bajocian). For a summary of the geology of the Yorkshire Jurassic, see Hemingway and Knox (1973).

Spores were recovered from the material by selecting (if possible) one sporangium of each taxon, macerating it in Schulze's reagent, and neutralizing with ammonia. For light microscopy, macerated fossil spores were mounted in glycerine jelly and sealed with paraffin wax. The slides were examined with a Leitz Ortholux microscope. For scanning electron microscopy (SEM), the samples were dehydrated in a graded ethanol and acetone series, placed on a standard specimen stub and air dried. They were coated with gold, and both viewed and photographed with a Camscan.

Most of the material is kept at The Natural History Museum, London (prefix V). One specimen is kept at the Laboratory of Palaeobotany and Palynology, University of Utrecht, the Netherlands (prefix S).

SYSTEMATIC PALAEONTOLOGY

Genus *OSMUNDOPSIS* Harris, 1931

Osmundopsis hillii sp. nov.

Plate 1, figures 1–5; Plate 4, figures 1, 6–7

Derivation of name. After Dr C. R. Hill who collected the material.

Holotype. V.60952 (Pl. 1, fig. 1); V.60953 (Pl. 1, fig. 2) is its counterpart; from Hasty Bank, Yorkshire, England; Saltwick Formation (Aalenian).

Diagnosis. Fertile leaf or leaf fragment with a slender, longitudinally striated rachis bearing widely spread subopposite branches arising at a wide angle. Branches probably equivalent of pinnules. 'Pinnules' up to 5 mm long, 1.5 mm wide, consisting of a narrow midrib bearing alternate, minute protuberances, each covered with a group of up to eight sporangia. Sporangia pyriform or obovate, 400–500 μm $\times$ 200–300 μm . Cells of apical region thickened, vertical dehiscence slit. Spores trilete, globose; exospore granulate; granules *c.* 1 μm in diameter; triradiate scar distinct, long without a margo. Mean spore diameter 42 μm (measured range 36–45 μm).

Description. The holotype (V.60952; Pl. 1, fig. 1) shows a 40 mm long leaf fragment. Its 0.7 mm wide, longitudinally striated rachis bears subopposite 'pinnules', six on each side, arising at an angle of 70–85°. The pinnules are *c.* 5 mm apart. It is probably an apical fragment, as the angle at which the pinnules arise is larger basally than apically, and because the lower pinnules are larger (5 mm $\times$ 1.5 mm) than the upper ones (3 $\times$ 1.2 mm). The pinnules consist of a slender (0.1 mm wide) midrib bearing very short, alternate axes covered with up to eight sporangia. There are four groups of sporangia on each side of the midrib in the lower pinnules, three groups in the upper ones. The first group arises at the basiscopic side. The groups of sporangia are *c.* 0.8 mm wide; each sporangium being *c.* 0.4 mm long and 0.3 mm wide. Only one spore (44 μm in diameter; Pl. 4, fig. 6) has been recovered as the sporangia had all shed their spores.

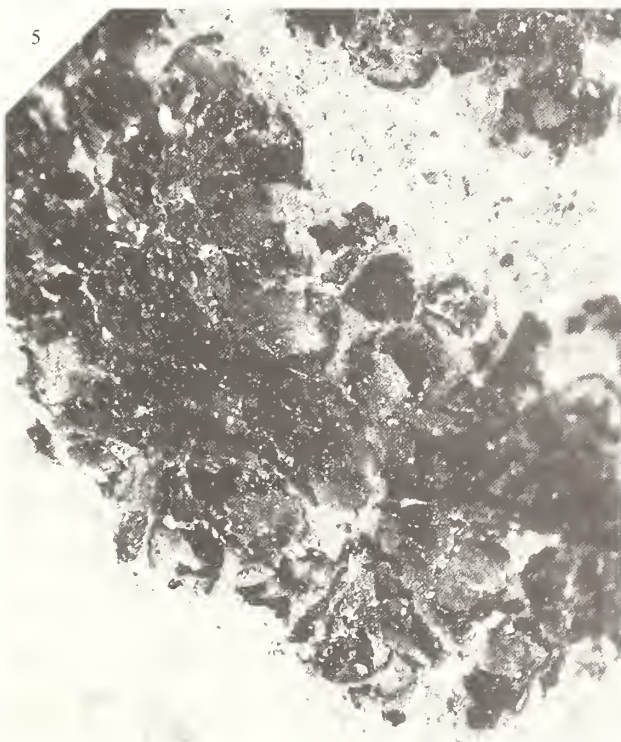
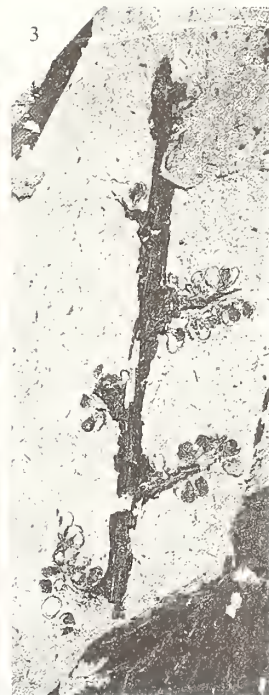
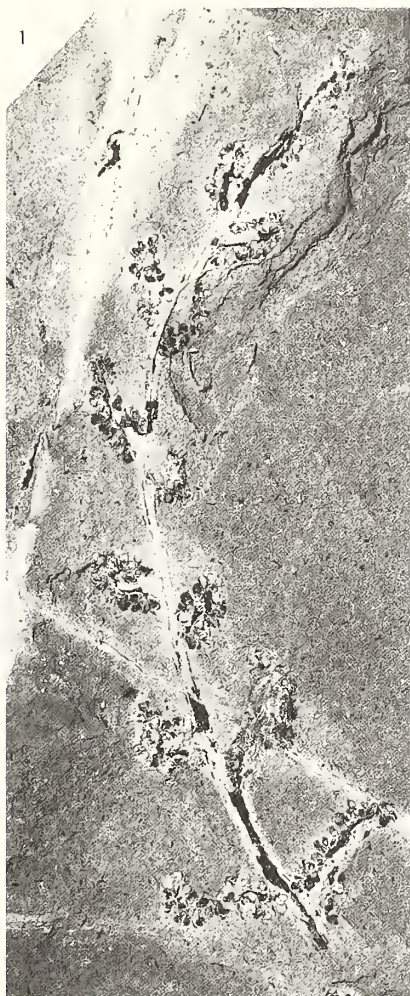
The counterpart (V.60953) shows a smaller part of the leaf fragment (only the apical part) but with an extra apical 5 mm including an extra, small cluster of sporangia on one side of the rachis (Pl. 1, fig. 2).

V.60954 and V.60955 (Pl. 1, fig. 3) are part and counterpart of a 15 mm long fragment. Its 0.8 mm wide, longitudinally striated rachis bears three pairs of subopposite to almost alternate pinnules, arising at an angle

EXPLANATION OF PLATE 1

Figs 1–5. *Osmundopsis hillii* sp. nov. 1, holotype, V.60952; $\times$ 3. 2, counterpart of holotype, V.60953; $\times$ 3. 3, V.60955; $\times$ 5. 4, sporangium showing dehiscence slit, V.60954\$1; $\times$ 150. 5, epoxy transfer V.60967, showing sporangia; $\times$ 30.

Figs 1–3 and 5, photographs courtesy of Dr C. R. Hill.



of *c.* 70° and *c.* 4 mm apart. The incomplete 'pinnules' (the apical parts are missing) are 2.5 mm long and 1.5 mm wide; their slender midrib bears three clusters of sporangia on each side. The sporangia are 400–500 μ m long and up to 300 μ m wide. Some show thickened apical cells and a vertical dehiscence slit (Pl. 1, fig. 4). Although these sporangia had also shed their spores, several spores were found sticking to the sporangial walls. They are included in the spore description. Spores were only studied under light microscopy (Pl. 4, figs 1, 7), and so it was impossible to see if the granules were fused in an irregular pattern as in *O. sturii*.

V.60956 shows a 25 mm long fragment, closely associated with sterile foliage of *Cladophlebis harrisii*. The 0.8 mm wide, longitudinally striated rachis is covered with seven pairs of almost opposite pinnules, arising at 80–90°, only 2–3 mm apart. The pinnules are *c.* 3 mm long and 1.2–1.5 mm wide and consist of a slender midrib with three alternate clusters of sporangia (first one on basiscopic side). The sporangia are 500 $\times$ 300 μ m. Again only a few spores could be recovered.

V.60967 is an epoxy resin transfer of one pinnule, 3 mm long, 1.2 mm wide, showing three clusters of sporangia on each side. This specimen demonstrates the apically thickened cells and the vertical dehiscence slit (Pl. 1, fig. 5).

Remarks. Although only a few specimens are present, the material differs so much from any known species of *Osmundopsis* that it is necessary to describe it as a new species. The main differences from other, well-known species are the small size of the 'pinnules', only up to 5 mm long (for instance, *Osmundopsis sturii* and *O. plectrophora*, such as from the Liassic of Greenland, have pinnules that are over 10 mm long) and the greater distance between the pinnules (see Table 1). In *O. hillii* there is always some distance between the pinnules, while in the other two species they can be almost in contact. Finally, the size of the sporangia in *O. hillii* is significantly smaller than in the other species (only 500 μ m long, *versus* up to 800 μ m in the other species). The differences from other *Osmundopsis* species are discussed below under *O. sturii*. For comparisons see also Table 1.

Sterile foliage. On V.60956, *O. hillii* is closely associated with *Cladophlebis harrisii* van Cittert, 1966 (this species was mistakenly described in Harris (1961) as *Selenocarpus muensterianus*). This sterile foliage is also present on the holotype, together with other fossils, such as the conifer *Elatides thomasi* and the dicksoniaceous fern *Dicksonia mariopteris*, the fertile foliage of which is well-known (see Harris 1961). *Cladophlebis harrisii* (Pl. 2, fig. 1) is quite common throughout the whole Hasty Bank section (section S2, see Hill 1974) where *Osmundopsis hillii* has been found. No other fern in which the fertile foliage is unknown occurs in this section; therefore, Dr Hill (pers. comm.) and I are of the opinion that *O. hillii* is the fertile foliage of *Cladophlebis harrisii*.

Osmundopsis sturii (Raciborski) Harris

Plate 2, figures 2–4; Plate 3, figures 1–3; Plate 4, figures 2–5; Text-figure 1

Material. Apart from the material from the Cayton Bay Gristhorpe bed described by Harris (1961, 1977), there are three more specimens from this locality that were found by J. D. Lovis, and one from Cloughton Wyke (*Solenites* bed). Moreover, there is a specimen in the collection at Utrecht. All these specimens will be described here.

Description. V.63876a/b is part and counterpart of a 30 mm long fragment (Pl. 2, figs 2, 4). The 0.5 mm wide, longitudinally striated rachis bears subopposite secondary branches that probably represent pinnules. They are 2 (in the apical region) to 3 mm apart (in the more distal region). These 'pinnules' consist of a thin axis covered by numerous sporangia. The sporangia are *c.* 400 μ m long and are probably immature; they yielded masses of thin-walled spores that could not be separated. The 'pinnules' are 5–7 mm long and 1–1.5 mm wide.

V.63877/63878 are part and counterpart (Pl. 2, fig. 3) of a 30 mm long fragment showing a small part of a

EXPLANATION OF PLATE 2

Fig. 1. *Cladophlebis harrisii* van Cittert. V.58754; $\times$ 1.

Figs 2–4. *Osmundopsis sturii* (Raciborski) Harris. 2, V.63876a and b; $\times$ 1. 3, V.63877 and V.63878; $\times$ 2. 4, V.63876a; $\times$ 5.



longitudinally striated rachis. There are eight secondary branches or 'pinnules' on one side of the rachis and only one on the other side; they are 3 mm apart, 8–10 mm long and 1.5 mm wide. They consist again of a thin axis covered with numerous pyriform or obovate sporangia, up to 500 μm long. They yielded masses of almost mature spores.

V.63875, from Cloughton Wyke, shows two pinna fragments lying next to each other (Pl. 3, fig. 1) and, slightly apart, an apical pinna fragment that probably belongs to the same frond. If they were originally attached, the total length would have been over 35 mm. The pinna rachises are 0.5–0.7 mm wide and show longitudinal striations. The secondary branches or 'pinnules' arise at a distance of 2.0–3.5 mm and are subopposite. Their maximum length is 10 mm, maximum width 1.5 mm (in the apical part the pinnules are crowded, sometimes even touching each other, and they are smaller). Again they show a thin axis covered with numerous, up to 600 μm long, pyriform sporangia. The sporangia clearly show that the cells of the whole apical region are thickened (Pl. 3, fig. 2). The sporangia yielded numerous, almost mature spores.

V.63934 shows several parallel pinnule fragments almost touching each other. The longest fragment is 8 mm long and 2 mm wide. The thin axes are covered with numerous pyriform sporangia that are 500–600 μm long and 300–400 μm wide. The sporangia yielded numerous spores.

V.63990 is a box with loose sporangia fallen from various specimens. It showed typical sporangia (Pl. 4, fig. 2) and mature spores, sometimes with a margo (thickening along the trilete mark; see Pl. 4, fig. 4).

S.7509 (Pl. 3, fig. 3) shows a 20 mm long pinna fragment, axis 1 mm wide, consisting of seven pairs of opposite, well-separated (c. 2 mm apart) 'pinnules' that are up to 10 mm long, and 1.5 mm wide. The thin axis of the pinnules is covered with numerous sporangia that yielded good spores. These spores and the ones from Harris' (1961) material were described in detail by van Konijnenburg-van Cittert (1978). The spores recovered from the other specimens described here agree in all aspects with this description, but show a slightly greater size, which may be due to the fact that only completely mature grains have been measured in this study.

Spores trilete, more or less spherical in equatorial outline. Laesurae distinct, narrow, sometimes bordered by a thin margo. Exine about 1.5 μm thick, covered with fused granules forming an irregular pattern.

Mean spore diameter c. 48 μm (extremes measured 42–54 μm). Mean spore diameter in the previous description was 42 μm (extremes 32–52 μm). This difference is mainly caused by the absence of small spores in the new material. For spore illustrations, see Plate 4, figures 3–5 and Text-figure 1.

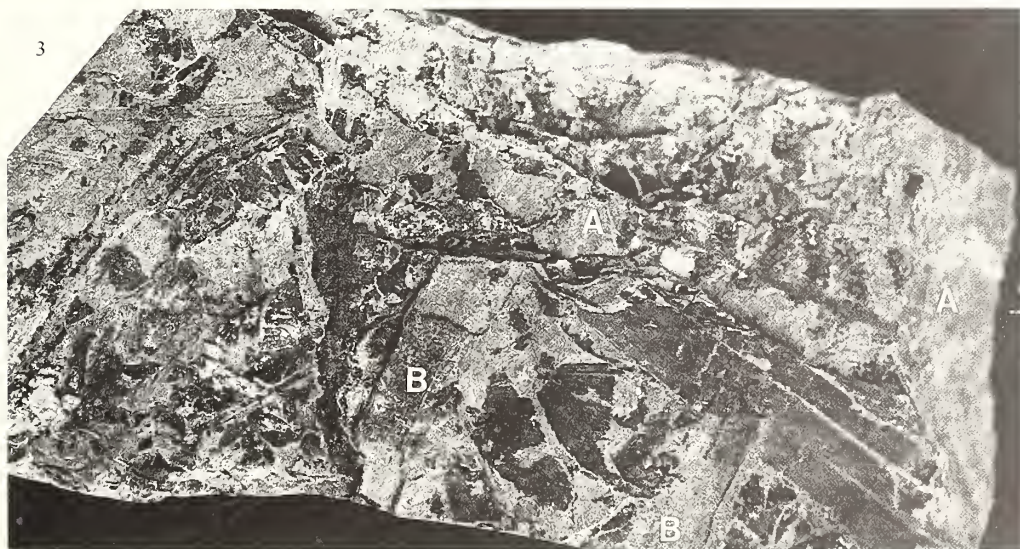
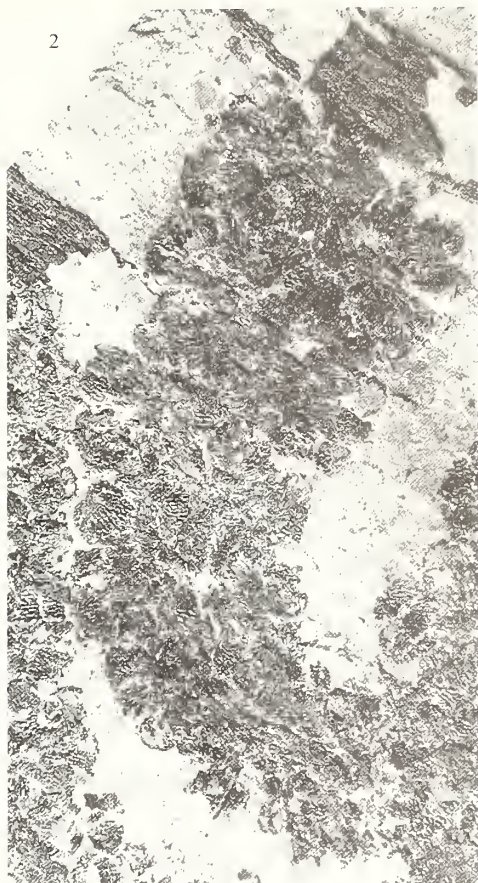
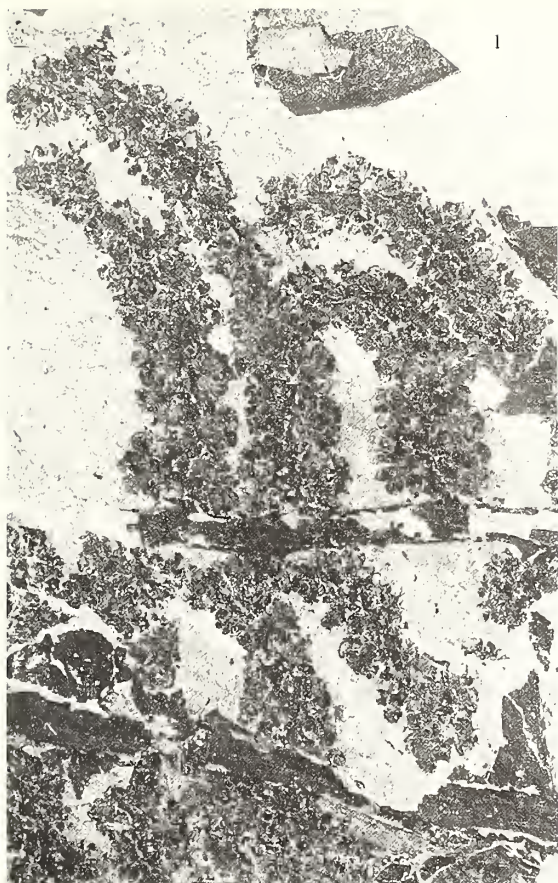
Remarks. The new material described here agrees in all details with the two specimens described by Harris (1961) and discussed by Harris (1977). There is no doubt about the absence of lamina, so their attribution to *Osmundopsis* is certain. Harris (1961, 1977) stated that, although there are large differences in preservation between the Yorkshire specimens and the original Polish material, there are no fundamental differences between them. Therefore, he attributed his material to *O. sturii*. Similar material from Iran was described by Kilpper (1964) as *O. cf. plectrophora*. Recent studies (Schweitzer *et al.* in press) have demonstrated, however, that this material is indistinguishable from *O. sturii*.

Sterile foliage. Another problem is the sterile foliage that belonged to this fertile material. It appears that none of the *Todites* or *Cladophlebis* species from the Gristhorpe bed at Cayton Bay (and from the *Solenites* bed at Cloughton Wyke) is available as sterile foliage; only fertile material is known. Lovis collected some sterile foliage from Cayton Bay that he thought might have belonged to *Osmundopsis* (Pl. 5, figs 1–4). However, its venation (Pl. 5, figs 2–3; Text-fig. 2) is unlike that seen in either *Cladophlebis* or *Todites*, and resembles much more the venation of the dicksoniaceae genus *Eboracia*. Indeed, when studying the material in detail, it proved that, although some of the specimens were considerably larger than normal *Eboracia lobifolia*, others showed all the characteristic features of that species, including the forked basal pinnule (Pl. 5, fig. 1). As

EXPLANATION OF PLATE 3

Figs 1–3. *Osmundopsis sturii* (Raciborski) Harris. 1, V.63875; $\times 7.5$. 2, V.63875, showing thickened apical cells; $\times 20$. 3, S.7509B, *O. sturii* (between A and A), associated with *Cladophlebis denticulata* pinnules (between B and B); $\times 2.5$.

Figs 2–3, photographs courtesy of Prof. Dr H. Kerp.



intermediate forms were also present, I think that all this material must be included in *Eboracia lobifolia*. The main difference between the new material and *E. lobifolia* as described by Harris (1961) lies in the pinnule size (up to 11×5 mm, see Pl. 5, fig. 2; while Harris gives 9×3 mm as the largest size) and the fact that in those large pinnules the base is always contracted on both sides (Pl. 5, figs 2, 4). In *E. lobifolia* the base is usually well constricted on the upper side, and only slightly or not at all on the lower side. Moreover, in the new material the large pinnules are often not lobed apart from the prominent basal lobe on both sides (Pl. 5, figs 3–4). The margin is in these cases only slightly wavy or even almost straight. The prominent basal lobe is supplied by one or more veins that arise from the pinna rachis rather than the midrib. In Harris' description there is only one such vein (twice forked) arising from the pinna rachis while in the new material there are sometimes more veins arising from the pinna rachis (see Text-fig. 2). But, as said above, some of the specimens are typical *Eboracia lobifolia* (Pl. 5, fig. 1), and intermediates are present as well (Pl. 5, figs 3–4).

Van Konijnenburg-van Cittert (1978) mentioned the presence of small sterile *Cladophlebis denticulata* fragments on S.7509 (Pl. 3, fig. 3). The Iranian *Osmundopsis sturii* material is almost certainly linked with *C. denticulata* leaves with relatively small pinnules. On the three Cayton Bay specimens described here, *O. sturii* was the only fossil present, but on the Cloughton Wyke specimen *C. denticulata* was also present. Therefore, it is possible that the artificial form-species *C. denticulata* consists of two natural taxa, one (often with large pinnules) linked with *Todites denticulatus*, and one (with relatively small pinnules) linked with *O. sturii*.

COMPARISONS

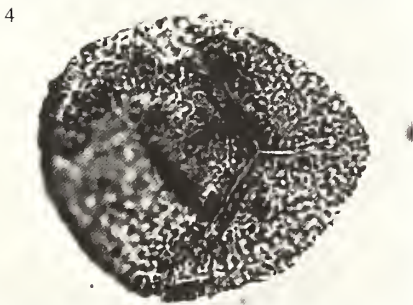
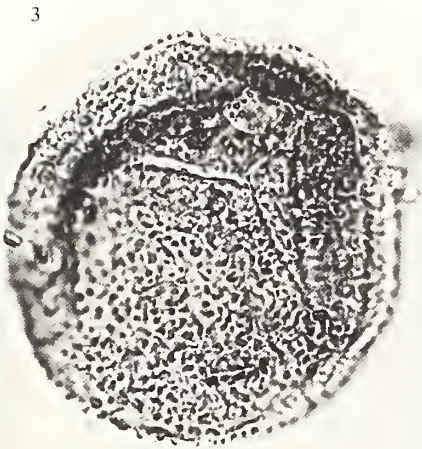
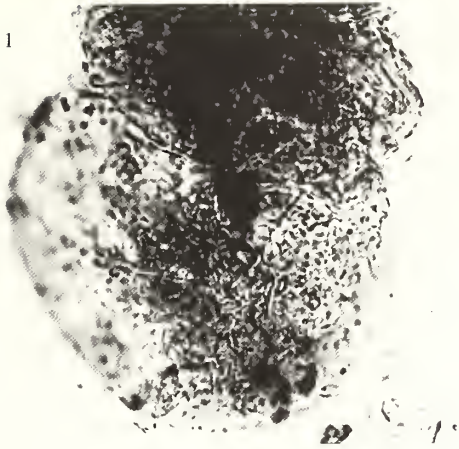
Osmundopsis hillii is easily distinguished from *O. sturii* by its smaller 'pinnule' size and the comparatively large distance between the pinnules. The whole pinna has a much looser appearance than in *O. sturii*. This is also caused by the fewer sporangia present in each pinnule. Indeed, in *O. hillii* the tertiary, very short branches (protuberances) are early recognizable and the number of sporangia per protuberance (and thus the number of sporangia per group) is never more than eight, while in *O. sturii* the tertiary branches are almost unrecognizable as they are covered by numerous sporangia. The separate groups of sporangia are easily seen in *O. hillii* (Pl. 1, figs 3, 5) while they cannot be recognized in the Yorkshire *O. sturii* material (in the Iranian material they can sometimes be seen in completely mature specimens). Finally, the sterile foliage attributed to *O. hillii* (i.e. *Cladophlebis harrisii*) is different from any other known *Cladophlebis* species (van Cittert 1966).

Osmundopsis microcarpa (Raciborski) Harris, from the Liassic of Poland, might have been young and/or apical fragments of *O. sturii* (see Harris 1977). *O. prigorovskii* Krystofovich and Prynada, 1933 may also be similar (Harris 1961). *O. prynadae* Delle, 1967 is also very similar to *O. sturii* and is associated with *Cladophlebis denticulata* leaves. This material (there is only one specimen) might very well be an immature *O. sturii* fragment; the fact that the spores are small ($25 \mu\text{m}$) and almost smooth may support this view. *Osmundopsis nipponica* Kimura and Tsujii, 1980 is also very similar to *O. sturii*, differing only in slightly less elongated secondary branches and smaller sporangia. It is, however, possible that all these species are real species that differ mainly in their sterile foliage. But as many of these sterile leaves are not yet known, I cannot make a definite statement.

EXPLANATION OF PLATE 4

Figs 1, 6–7. *Osmundopsis hillii* sp. nov. spores. 1, V.60945S2; $\times 1000$. 6, from holotype, V.60952S1; $\times 500$. 7, V.60954S2; $\times 500$.

Figs 2–5. *Osmundopsis sturii* (Raciborski) Harris. 2, V.63990, typical sporangium with spores; $\times 100$. 3, LM micrograph of spore from V.63878S2; $\times 1000$. 4, LM micrograph of spore with margo, V.63990S1; $\times 1000$. 5, LM micrograph of group of spores, V.63878S2; $\times 500$.





TEXT-FIG. 1. *Osmundopsis sturii* (Raciborski) Harris; SEM photo of spores from S.7509; $\times 800$.



TEXT-FIG. 2. Schematic drawing of the venation in large pinnules of *Eboracia lobifolia*; (Phillips) Thomas; c. $\times 5$.

O. plectrophora, from the Liassic of Greenland (Harris 1931), differs from both *O. hillii* and *O. sturii* in its longer stalked sporangial groups and broader sporangia (up to 0.6 mm; while they are only 0.3 mm in *O. hillii* and 0.4 mm in *O. sturii*).

O. scythica Stanislavski, 1971 resembles *O. plectrophora* both in its larger sporangia and in the sterile leaves with a lobed basal pinnule that overlies the rachis. The difference between the two species lies mainly in the venation of the sterile leaves: the secondary veins in *O. scythica* often fork twice, while they fork only once (apart from the basal vein) in *O. plectrophora*. Here again, we see

EXPLANATION OF PLATE 5

Figs 1–4. *Eboracia lobifolia* (Phillips) Thomas. 1, V.63942a; small leaf fragment with a typical basal pinnule (arrow); $\times 2$. 2, V.63940; large pinnules, showing venation and contracted bases on both sides; $\times 2.5$. 3, V.63939b; two pinnae, pinnules with contracted bases only on the upper sides; $\times 2.5$. 4, V.63935; pinna, typical of the present material; $\times 1$.

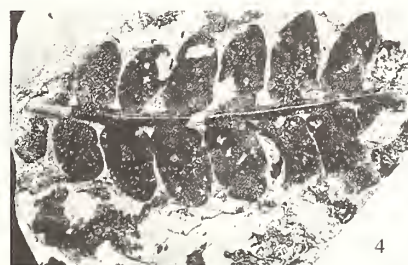
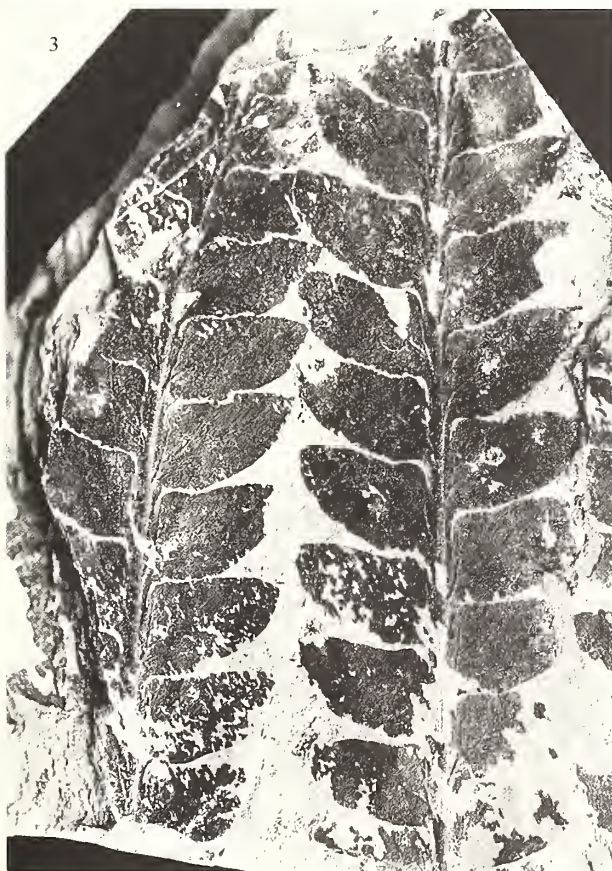


TABLE 1. Comparison of *Osmundopsis* species

Species	<i>O. hillii</i>	<i>O. sturii</i>	<i>O. plectrophora</i>	Antarctic <i>Osmundopsis</i>
Distance between 'pinnules'	3–5 mm	2–3 mm	3 mm	2 mm
Length of fertile 'pinnules'	Up to 8 mm	Up to 10 mm	Up to 20 mm	Up to 3 mm
Number of sporangia/cluster	Up to 8	Up to c. 20	Up to c. 12	?
Maximum sporangium size	500 × 300 µm	600 × 400 µm	800 × 500 µm	?
Mean spore diameter	42 µm	48 µm	50 µm	?

the main difference between two *Osmundopsis* species in the sterile leaf and not in the fertile part.

Taylor *et al.* (1990) described some sterile and fertile osmundaceous material from the Upper Triassic of Antarctica, without formally naming it. The fertile material consists of reduced, modified pinnae c. 10 mm long, arising suboppositely at c. 2 mm from each other from a c. 5 mm wide rachis. Each fertile pinna is a non-laminated unit bearing side branches (only up to 3 mm long), about 2 mm from each other with a thin rachis covered with tightly compacted clusters of sporangia. No details of the sporangia or spores have been described or are visible from the illustrations.

Osmundopsis hillii, *O. sturii*, *O. plectrophora* and the Antarctic material are compared in Table 1.

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NEW OBSERVATIONS ON THE ECOLOGY OF THE PERMIAN CAPITAN REEF, TEXAS AND NEW MEXICO

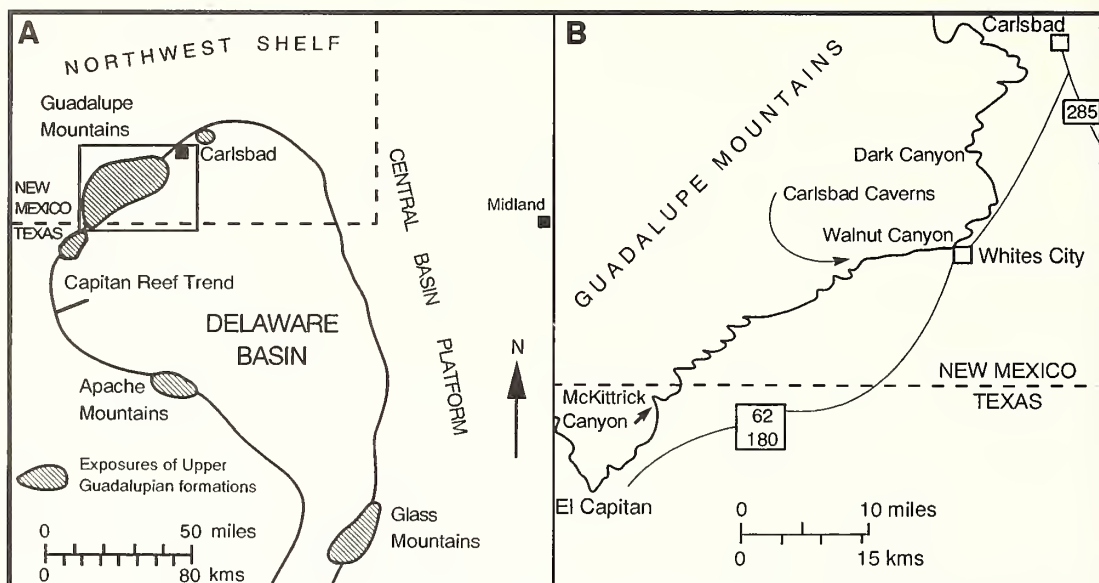
by RACHEL WOOD, J. A. D. DICKSON and BRENDA L. KIRKLAND

ABSTRACT. The Permian Capitan reef was a predominantly heterotrophic ecosystem strongly differentiated into open surface and cryptic communities. Unlike modern phototrophic corallgal reefs, most of the preservable epibenthos was housed within the cryptos and zonation developed only in the shallow parts of the reef. Contrary to established opinion, most sphinctozoan sponges did not grow upright to form a baffling framework but rather were pendent cryptobionts, as were nodular bryozoans and rare solitary rugose corals and crinoids. Indeed, many members of the cryptos were obligate cryptobionts. Much of the Middle Capitan reef framework was constructed by a scaffolding of large frondose bryozoans, with the subsidiary platy sphinctozoan *Guadalupia zitteliana*. Bathymetrically shallow areas of both the Middle and Upper Capitan reef, however, were characterized by platy sponges. In parts of the Upper Capitan, some platy sponges (*Gigantospongia discoforma*) reached up to 2 m in diameter and formed the ceilings of huge cavities which supported an extensive cryptos.

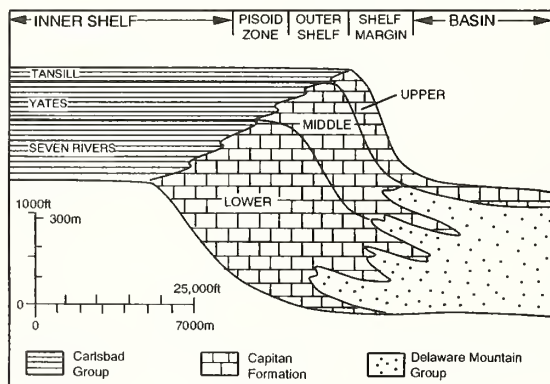
In the absence of destructive forces (both biotic and physical) prevalent on modern reefs, the relatively fragile Capitan reef remained intact after the death of the constructing organisms. Rigidity was imparted to this community by a post-mortem encrustation of *Tubiphytes* and *Archaeolithoporella*, together with microbial micrite. The resultant cavernous framework was partially infilled with sediment and preserved by syndimentary intergrowth of aragonitic botryoids and *Archaeolithoporella*. Extensive cement precipitation was favoured by a number of factors including deep anoxia, which generated upwelling waters with elevated alkalinity. Although the accumulation rate of the Capitan may have been comparable to that of modern corallgal reefs, both the trophic structure and relative contributions of inorganic and organic carbonate were profoundly different.

CALCIFIED metazoans have aggregated to form reefal buildups throughout the Phanerozoic, but during this time many evolutionary innovations as well as extinction events have exerted profound changes on the biotic constituents and trophic structure of reef communities. Modern corallgal reefs are highly complex, specialized ecosystems driven by photosymbiosis and regulated by intense predation. Yet there is little evidence (except possibly in tabulate corals) for the existence of widespread photosymbiotic reef communities before the acquisition of zooxanthellae by scleractinian corals in the late Triassic (Wood 1993). Moreover, most predator groups responsible for the regulation of modern reef community structure did not appear until the late Mesozoic or early Cenozoic (Wood 1993, 1995). We can therefore expect Palaeozoic reefs to have had a very different ecological caste to modern representatives.

The Permian Capitan reef, West Texas and New Mexico, forms one of the finest examples of an ancient rimmed carbonate shelf. The reef, as expressed in the massive Capitan Limestone (Hayes 1964) and associated upper Guadalupian carbonate platform, defines the margin of the Delaware Basin (Text-fig. 1). Equivalent shelf units form reservoirs on the northern and eastern sides of the basin (Ward *et al.* 1986). Although most of the Capitan reef is subsurface, spectacular exposures are known from the Guadalupe, Apache, and Glass Mountains. The east side of the southern Guadalupe Mountains represents an erosionally modified depositional profile of shelf to basin sediments which were exhumed during the late Cenozoic, with the reef itself marking a prominent



TEXT-FIG. 1. A, map of the Permian Delaware Basin showing exposures of upper Guadalupian formations and location of the Capitan reef trend; B, detail of the Capitan reef front, Guadalupe Mountains with locations mentioned in the text (modified from King 1948).



TEXT-FIG. 2. Schematic cross section showing shelf-to-basin correlations of the Capitan Formation and equivalents (after Babcock and Yurewicz 1989) and subdivision of the shelf (after Esteban and Pray 1983).

topographical boundary between deep-water basinal deposits and shallow shelf sediments to the north-west.

During the Late Permian, the Delaware Basin was almost entirely surrounded by land (Ward *et al.* 1986) and lay a few degrees north of the equator on the western side of Pangaea (McKerrow and Scotese 1990). The area was intermittently arid, as evidenced by large evaporite deposits in the basin and its fringing lagoons (Adams and Rhodes 1960). Indeed, the basin and shelf deposits of the Delaware Basin were sealed and preserved by latest Permian (Ochoan) evaporites.

The Capitan reef is the youngest of a series of shelf-margin complexes which developed around the Delaware Basin over a total period of some 12 My (Garber *et al.* 1989). The reef forms prograding beds of generally 20–40°; but which may locally be vertical (Bebout and Kerans 1993).

These massive limestones served to mark an abrupt transition between the basin floor and shelf which has been suggested to have progressively shallowed (Cys 1971; Babcock 1977; Toomey and Babcock 1983): by the end of Capitan Limestone deposition water depth in the Delaware Basin is estimated to have reached 450–600 m (Yurewicz 1976). There is also an abrupt contact between the massive limestones and the bedded grainstones and packstones of the outer shelf (Text-fig. 2). These shelf sediments contain a biota characteristic of restricted, slightly hypersaline conditions and their mud content increases shelfwards suggesting quiet, back-reef lagoonal deposition (BLK, pers. obs.).

Classic exposures of the Capitan reef and its associated sediments are known from a series of canyons running parallel and perpendicular to the reef-margin. Some canyons, such as McKittrick, display nearly complete sections through the platform margin, thus allowing interpretation of both the changing depositional profile and the nature of the transition from the reef to associated sediments. Notwithstanding such excellent exposure, however, many aspects of the nature of the reef margin have remained enigmatic. The crucial facies which controlled sedimentation across the late Guadalupian shelf margin is the massive Capitan Limestone, yet little is known as to its mode or depth of formation. The Capitan Limestone may also have controlled deposition of the shelfward lithologies of the Carlsbad Group (Seven Rivers, Yates and Tansill formation; BLK, pers. obs.).

The Capitan Limestone ranges from 100–200 m thick and has been subdivided into Lower, Middle and Upper members (Babcock 1977; Yurewicz 1977) equivalent to the Seven Rivers, Yates and Tansill formations respectively (Text-fig. 2). The Capitan Limestone contains a diverse and distinctive biota estimated at some 350 taxa (Girty 1908; King 1948; Newell *et al.* 1953; Fagerstrom 1987), which includes abundant calcareous sponges (the polyphyletic chambered spinctozoans and non-chambered inozoans), putative algae, bryozoans, brachiopods and several enigmatic organisms such as *Tubiphytes*. Interpretations as to whether any of these organisms were capable of producing a wave-resistant framework have remained at the heart of the Capitan controversy. Workers who consider a rigid framework to have been present compare the Capitan to a modern corallgal barrier reef (Crandall 1929; Lloyd 1929; Johnson 1942; Newell *et al.* 1953; Newell 1955; Klement 1966; Cys 1971; Cronoble 1974; Yurewicz 1977; Mazzullo and Cys 1978; Fagerstrom 1987; Babcock and Yurewicz 1989; Kirkland-George 1992; Kirkland *et al.* 1993). In contrast, Achauer (1969) and Dunham (1970, 1972) proposed the Capitan Limestone to have formed as a linear bank of baffling metazoans growing in deeper waters. They considered that few fossils are in growth position and therefore inferred that the community was incapable of creating a wave-resistant framework. Others have emphasized the constructional role of extensive algal encrustation and early cementation in producing a rigid framework which bore considerable relief (Babcock 1974, 1977; Yurewicz 1976, 1977; Schmidt 1977; Mazzullo and Cys 1978).

Interpretations as to the depth at which the Capitan Limestone formed are critical to late Guadalupian physiography, but remain a matter of intense controversy. Such uncertainty is exemplified by the number of competing bathymetric profile models proposed for the shelf margin. Newell *et al.* (1953) depicted a profile similar to a modern barrier-reef with the Capitan growing to sea-level. Dunham (1972) proposed the pisolite facies belt landwards of the reef to be a series of subaerially exposed shoals, whilst the reef grew below wave base and had little positive topographical relief. Kirkland (1992) included both exposed tidal flat facies and a reef growing to sea-level in her reconstruction of the shelf margin. These models cannot be reconciled: whether the reef formed in turbulent surface waters or in the more tranquil depths is of fundamental ecological importance.

METHODS

Detailed field observations of biotic interactions were made on naturally weathered surfaces parallel to reef growth on the Permian Reef Geology Trail, McKittrick Canyon which exposes approximately 140 m of the Middle Capitan Limestone (middle and upper Yates-equivalent). Acid-etched surfaces of approximately 43 m of upper Upper Capitan Limestone (lower Tansill-equivalent) were studied at the mouth of Walnut Canyon, Whites City. Hand specimens collected from both these localities were either serially slabbed and polished or thin sectioned. Additional

observations of reef fabrics were made in the Left Hand Tunnel of Carlsbad Canyon. The zone foraminifera *Polydioexodina* is found above these exposures indicating a lower middle Capitan or older age (BLK, pers. obs.).

Studied material has been lodged in the Sedgwick Museum, Cambridge (prefix SMX) and the Dept of Geology, University of Texas, Austin (prefix STC).

ECOLOGY

The massive Lower and Middle Capitan Limestone contains fewer putative algae than the Upper Capitan and has been interpreted to be a shelf-edge accumulation of various suspension feeders (especially calcareous sponges and bryozoans) living in moderately deep water of low turbidity (Yurewicz 1976, 1977; Babcock and Yurewicz 1989). Yurewicz concluded that the Middle Capitan Limestone exhibited 20–60 per cent. boundstone (the remainder being packstone and grainstone) in which he identified three distinct fabrics: two dominated volumetrically by the encrusting putative rhodophyte *Archaeolithoporella* and one by the problematical branching or encrusting ?alga *Tubiphytes*. Yurewicz proposed that all boundstone fabrics initiated upon erect skeletal organisms, which formed the framework for subsequent *Archaeolithoporella* encrustation and inorganic cementation. He believed that the Lower Capitan reef was 45 m deep at its crest, rising to 30 m by the end of Middle Capitan time. He found little evidence for zonation.

A further reef fabric in the Middle Capitan Limestone was identified along the Permian Reef Geology Trail, McKittrick Canyon: patchily developed thickets of *Tubiphytes* and *Acanthocladia* (a ramose bryozoan), with voids infilled with cement and laminated internal sediment (Kirkland *et al.* 1993). They noted the restriction of the ?alga *Collenella* to the shallowest parts of the reef – those nearest to the outer shelf. Apart from this observation, they also concluded that little zonation is evident in the Middle Capitan Limestone as exposed in the Permian Reef Geology Trail.

The Upper Capitan Limestone has been described as being dominated by abundant and diverse frame-building calcareous algae growing in intimate association with inorganic cement (Babcock 1974, 1977). Babcock concluded that a greater proportion of this upper part of the reef was in situ, with 50–75 per cent. boundstone fabrics. He identified four boundstone fabrics: *Collenella*/*Parachaetetes*, *Tubiphytes*, *Tubiphytes*-sponge and *Archaeolithoporella*/nodular. He concluded that the Upper Capitan grew to within 10 m of sea level, and showed marked algal zonation.

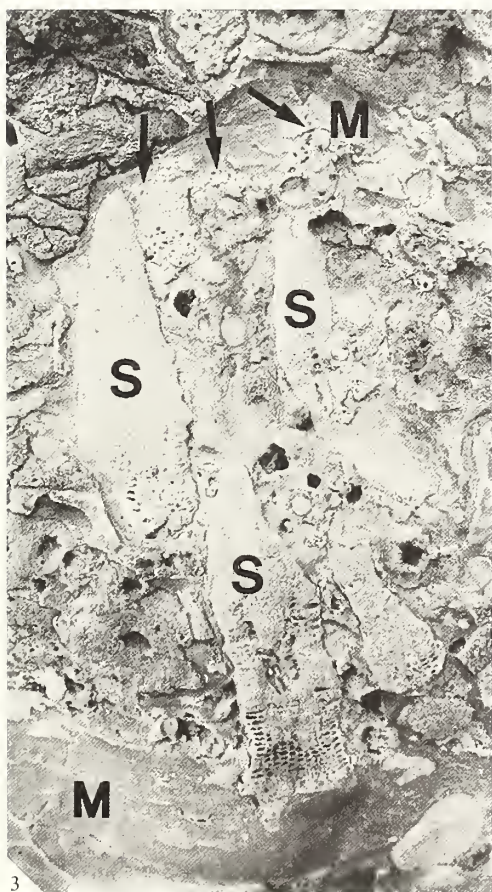
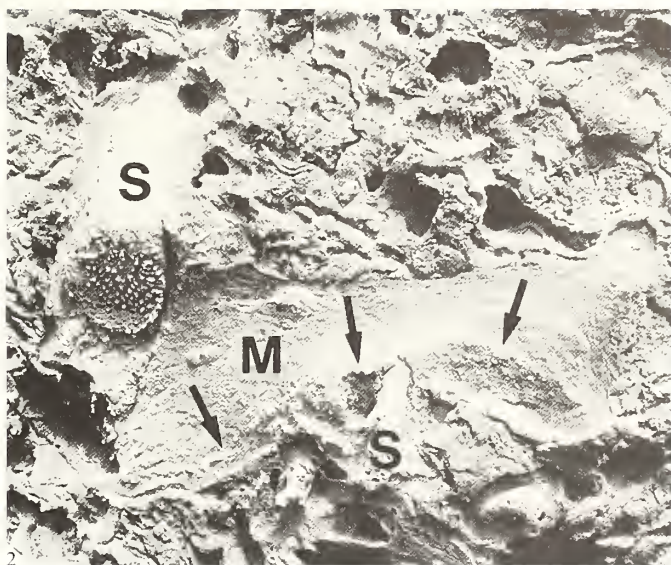
Established ecological reconstructions have thus emphasized the role of various baffling branching or solitary organisms (sphinctozoan sponges, bryozoans and *Tubiphytes*) and massive putative algae (*Collenella*, *Parachaetetes* and *Solenopora*) in the construction of the Capitan reef, together with the binding and encrusting contribution of *Archaeolithoporella* and extensive early marine cementation. Babcock and Yurewicz (1989) emphasized that cement growth was prolific, initiating not only within micropores and in large cavities below the surface of deposition, but also as crusts or nodules directly upon the sea floor.

EXPLANATION OF PLATE 1

Frondose bryozoan-sponge community

Figs 1–4. Weathered surfaces parallel to reef growth from the Middle Capitan Limestone, McKittrick Canyon, showing latticework of bryozoans (arrowed) forming cavity boundaries which support a cryptos of sphinctozoan sponges (S). Note post-mortem encrustation of micrite (M). Remaining space is infilled by intergrown *Archaeolithoporella* and cement botryoids. Figs 1, 4, $\times 0.2$; Figs 2–3, $\times 1$.

Fig. 5. Weathered surface approximately perpendicular to reef growth showing bryozoan fronds (arrowed) clearly forming the framework for the subsequent precipitation of microbial micrite (M). Remaining cavity space has been infilled by late-stage sparry calcite; $\times 0.5$.



In this study we have identified five reef-building communities in the middle and upper Capitan Limestone. The (1), phylloid algal and (2), *Tubiphytes*-sponge communities of Babcock (1974, 1977) have been noted at the mouth of Walnut Canyon, Whites City between the elevations of 1130–1133 m and 1138–1143 m respectively. The (3), *Tubiphytes-Acanthocladia* community of Kirkland *et al.* (1993) was found in isolated patches throughout the Middle Capitan exposed at McKittrick Canyon, except in the uppermost 10 m of the reef. The most widespread reef fabrics encountered, however, represent two newly identified associations, here named the frondose bryozoan-sponge and platy sponge communities. They correspond in part to the previously described *Archaeolithoporella*-dominated communities (Babcock 1974, 1977; Yurwicz 1976, 1977; Babcock and Yurewicz 1989). Their distribution and ecology are described below.

Frondose bryozoan-sponge community

This community has been identified from the Middle Capitan Permian Reef Geology Trail in McKittrick Canyon, where it forms the bulk of discernible reef fabric from the base of the Capitan Limestone exposure (at an elevation of approximately 1905 m) to within approximately 10 m of the uppermost exposure of the Massive Member (Hayes 1964) at some 2050 m elevation, giving a total thickness of some 130 m. The same association has been found within the Upper Capitan Limestone at the mouth of Walnut Canyon, Whites City, where it occurs at the base of the exposure some 30 m below the highest contact between the reef and backreef. A similar fabric was also noted in the fallen blocks from the Left Hand Tunnel of Carlsbad Canyon, which are thought to be of Lower or Middle Capitan age.

Contrary to established opinion, the vast majority of calcified sponges (sphinctozoans) found at these locations are cryptic, projecting downwards into cavities (Wood *et al.* 1994). Most sponges are attached to the upper surface of crypts (Pl. 1, figs 1–4), whilst a few project from the walls or floors. Where holdfast structures are discernible, the sponges are commonly attached to frondose bryozoans (Pl. 1, figs 1–4) identified as *Goniocladia* sp., two species of *Fenestella* and cf. *Polypora* sp., or occasionally to the platy sphinctozoan *Guadalupia zitteliana* (Pl. 2, fig. 1). Polished serial-slabs reveal the ceilings and walls of crypts often to be supported by these highly convoluted fan- or plate-shaped metazoans (Text-fig. 3). The pervasive nature of the primary constructional role of the frondose bryozoans in particular is demonstrated by the tracing of vertical weathered surfaces parallel to reef-growth (Text-fig. 4), where the bryozoans commonly demark ceilings and walls of large crypts up to 0.5 m wide and 0.4 m high. Bryozoan fronds appear to have grown in varied orientations and are up to 0.25 m in any one dimension. They often show secondary thickening and inter-colony fusion.

Frondose bryozoans and *Guadalupia zitteliana* thus formed a community of erect, or horizontally projecting fans whose undersurfaces were colonized by an abundant cryptic epibenthos (Text-fig. 5A; Table 1). The preservable cryptos was dominated volumetrically by diverse solitary sphinctozoan sponges, especially *Lemonea cylindrica*, *Amblysiphonella* spp. and *Cystauletes* spp., which are commonly 50–100 mm long but may reach 200 mm. These sponges show some alignment, suggesting preferential growth possibly in response to prevailing current direction (Text-fig. 6). Small, nodular bryozoans (*Girtypora* sp. and *Fistulipora* spp.) up to 7 mm in diameter are also common crypt dwellers, and may be attached either directly to platy sponges or frondose bryozoans (Pl. 2, fig. 3), or to other cryptobionts. Rare, nestling small rugose corals, crinoid holdfast structures with associated stems and an unidentified massive encruster have also been identified within crypts (Table 1).

Much of the reef community shows evidence of multiple biological encrustation. Chains of pendent sphinctozoan individuals are common. Both the open surface community and cryptos are often covered by encrustations up to 40 mm thick of intergrown *Archaeolithoporella*, *Tubiphytes* and foraminiferans (Pl. 2, fig. 2), together with rare hexactinellids and weakly calcified encrusting sponges and soft-bodied encrusters (Pl. 2, fig. 1). There is also some evidence of microboring activity.

The metazoan reef community accounts for only a minor proportion of the total reef fabric, occupying approximately 7–17 per cent. of which 6–15 per cent. is occupied by the cryptic sponges. A substantial proportion of the reef fabric (25–50 per cent.) is now occupied by pale to mid-grey laminated micrite. This material has previously been interpreted as geopetal detrital sediment infill (Babcock 1974, 1977; Babcock *et al.* 1977; Kirkland *et al.* 1993). Close inspection, however, reveals that micrite occurs not only as cavity fill but also as an encrustation around the open-surface community (Pl. 1, figs 2–3, 5) and pendent cryptos (Pl. 1, figs 2, 4). The micrite has a layered, thrombolitic to peloidal texture in thin section (Pl. 2, fig. 4), and incorporates bioclastic debris. It is commonly encrusted by multiple generations of foraminifers (Pl. 2, fig. 4). The absence of an organic cellular texture and the incorporation of detritus implies a soft, mucoidal precursor rather than a rigid skeletal structure. We suggest this micrite to be of microbial origin (Wood *et al.* 1994) which grew incrementally and became lithified syndementarily. On the basis of its enveloping distribution around many skeletal elements of the reef fabric, this microbial micrite encrustation is proposed to have occurred after the death of the encrusted biota. The micrite would have served to lend considerable rigidity to an otherwise relatively fragile reef framework, forming an open network of interconnected cavities and tunnels.

Remaining cavity space (up to approximately 70 per cent.) was infilled by assorted bioclastic sediment, botryoids and intergrown *Archaeolithoporella*, botryoids and various late stage spars (Mruk 1989). Botryoids form grey and brown fans 10–50 mm in radius and nucleated on crypt ceilings, walls and floors as well as from the projecting cryptos (Pl. 2, fig. 1). Petrographic and isotopic analysis suggests an aragonitic precursor and marine origin (e.g. Loucks and Folk 1976; Mazzullo and Cys 1979; Mruk 1985, 1989). Several generations of isopachous radial calcite rimming cements 0.5–4 mm thick also encrust the surfaces of pendent cryptos and botryoids, postdating botryoid growth (M. Rahnis and BLK, pers. obs.). Remaining cavity space was infilled by various dolomites, late-stage sparry calcites, evaporite minerals and kaolinite (Scholle *et al.* 1992).

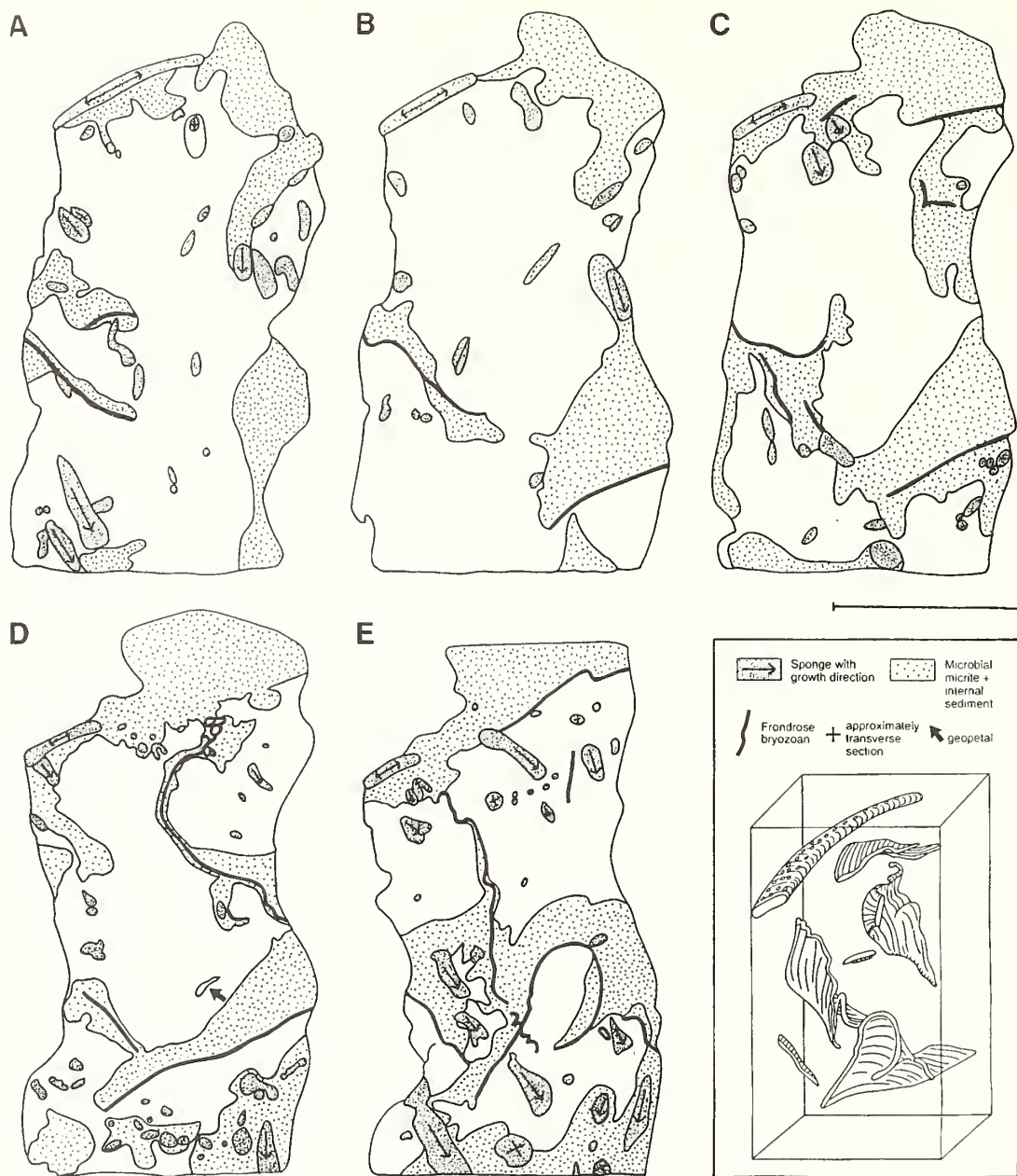
From these observations we infer the sequence of development of the frondose bryozoan-sponge community to have been:

1. Inter-connected large, convoluted fan-shaped bryozoan colonies and the platy sphinctozoan *Guadalupia zitteliana* grew projecting from the reef together with small thickets of branching acanthocladid bryozoans and *Tubiphytes* (Text-fig. 5A).
2. The undersurfaces of these platy metazoans formed open crypts which were colonized by an abundant biota dominated by pendent sphinctozoan sponges and small bryozoans.
3. The cryptos was encrusted by foraminiferans, *Tubiphytes* and *Archaeolithoporella*.
4. The entire epibenthic community was encrusted post-mortem by microbial micrite forming a rigid, open framework.
5. Cavity space was initially filled by sediment and the syn-sedimentary intergrowth of aragonitic botryoids and *Archaeolithoporella*, with the bulk of remaining space filled by botryoids. Some cavities remained entirely open.

Platy sponge community

A community dominated by platy sponges has been identified from the upper 10 m of the Middle Capitan reef on the Permian Reef Geology Trail, McKittrick Canyon (2050–2060 m elevation) and in fallen blocks within the reef foreslope thought to be equivalent to the Upper Capitan (Bebout and Kerans 1993). The platy sponges are the sphinctozoan *Guadalupia zitteliana*, which develops a convex morphology and may reach up to 0.25 m in diameter (Pl. 4, figs 1, 4). This community is associated with rare, small erect growths (up to 0.15 m high) of *Collenella*.

A further platy sponge community is well developed in the lower Upper Capitan Limestone between the elevations of 1133–1138 m (i.e. 10–5 m below the topmost exposure of the Capitan Limestone) at Walnut Canyon, Whites City. Here, the reef framework was dominated by very large individuals of the inozoan *Gigantospongia discoforma* (Pl. 3; Pl. 4, figs 2–3) and the sphinctozoan



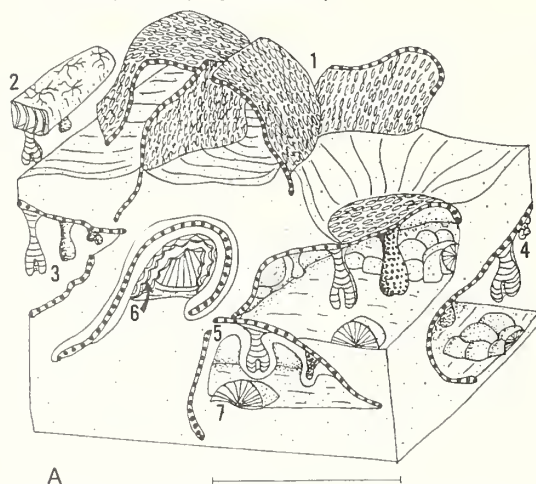
TEXT-FIG. 3. Tracings of serially slabbed polished surfaces (A-E) from the frondose bryozoan-sponge community cut perpendicular to horizontal from the Middle Capitan Limestone, McKittrick Canyon. STC-1-PmTx to STC-5-PmTx (corresponding to A-E respectively). Slabs are spaced approximately 15 mm apart. Note that frondose bryozoans commonly define crypt ceilings and walls, together with the platy sphinctozoan *Guadalupia zitteliana*. This framework was colonized by abundant cryptic sphinctozoan sponges. Both the reef framework and attached cryptos is enclosed by a post-mortem microbial micrite encrustation. A three dimensional reconstruction is given showing the convoluted nature of the bryozoan frond latticework. Scale bar represents 0.1 m.



TEXT-FIG. 4. Tracing of a weathered surface perpendicular to horizontal of the frondose bryozoan-sponge community from the Middle Capitan Limestone. Stop 15, elevation approximately 1905 m (6250 ft), Permian Reef Geology Trail, McKittrick Canyon. Note the lattice arrangement of the frondose bryozoans which commonly support crypt ceilings and walls, attendant cryptic calcified sponges, and encrusting nature of the microbial micrite. Modified from Wood *et al.* (1994). Scale bar represents 50 mm.

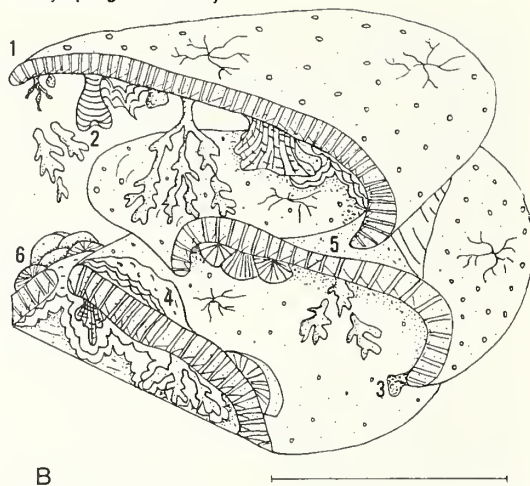
Guadalupia explanata. *G. discoforma*, although never more than 20 mm thick, grew up to 2 m in diameter. This species has also been found at Chinaberry and Hackberry Draws in the Guadalupe Mountains (Rigby and Senowbari-Daryan 1996). The less abundant *Gu. explanata* has a similar thickness, but reached a maximum diameter of 0.5 m. These sponges display laminar, convex, or convoluted morphologies, sometimes with marked downturned edges forming tunnel-like structures (Pl. 3, fig. 3). They were presumably attached by a site of limited size; no evidence of stacking, or mutual attachment of these platy sponges has been found. Microporous inhalant surfaces are on the underside and upper surfaces may bear traces of exhalant astrorhizal systems (Senowbari-Daryan 1990; Rigby and Senowbari-Daryan 1996). This orientation is constant in the field suggesting that these sponges are preserved in life position.

Frondose bryozoan-sponge community



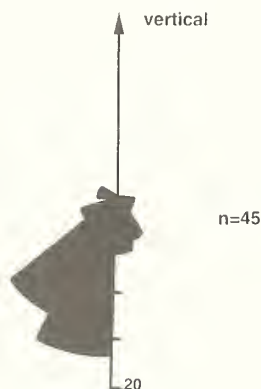
A

Platy-sponge community



B

TEXT-FIG. 5. Schematic community reconstructions. A, frondose bryozoan-sponge community: 1, frondose bryozoans; 2, platy sponge (*Guadalupia zitteliana*); 3, cryptic solitary sphinctozoans; 4, cryptic nodular bryozoans; 5, microbial micrite + bioclastic sediment; 6, *Archaeolithoporella*; 7, aragonitic cement botryoids. B, platy sponge community: 1, platy sponges (*Gigantospongia discoforma* + *Guadalupia zitteliana*); 2, cryptic sphinctozoans; 3, cryptic bryozoans; 4, *Archaeolithoporella*; 5, microbial micrite; 6, aragonitic cement botryoids. Scale bars represent 1 m.



TEXT-FIG. 6. Rose diagram showing preferential alignment of cryptic sphinctozoan sponges taken from tracing shown in Text-figure 4. Only sponges whose growth direction could be determined were included.

EXPLANATION OF PLATE 2

Photomicrographs of the Permian Capitan reef.

Fig. 1. Frondose bryozoan-sponge community, Middle Capitan Limestone, McKittrick Canyon, showing the sphinctozoan *Guadalupia zitteliana* forming a cavity ceiling. The undersurface has been colonized by various encrusters including soft-bodied or weakly calcified forms, and the solitary sphinctozoan *Cystauletes*, upon which botryoidal cement fans have nucleated; SMX 26221; $\times 6$.

Fig. 2. Platy sponge community, Upper Capitan Limestone, Walnut Canyon, showing two cryptic pendent *Girtypora* sp. bryozoans, later encrusted by *Tubiphytes* and *Archaeolithoporella*; SMX 26222; $\times 10$.

Fig. 3. Frondose bryozoan-sponge community, Middle Capitan Limestone, McKittrick Canyon, showing the frondose bryozoan *Goniocladia* sp. forming a cavity. The crypt is inhabited by a fisuliporid bryozoan; SMX 26223; $\times 5$.

Fig. 4. Frondose bryozoan-sponge community, Middle Capitan Limestone, McKittrick Canyon. Peloidal texture and encrusting foraminifera of putative microbial micrite; SMX 26224; $\times 15$.

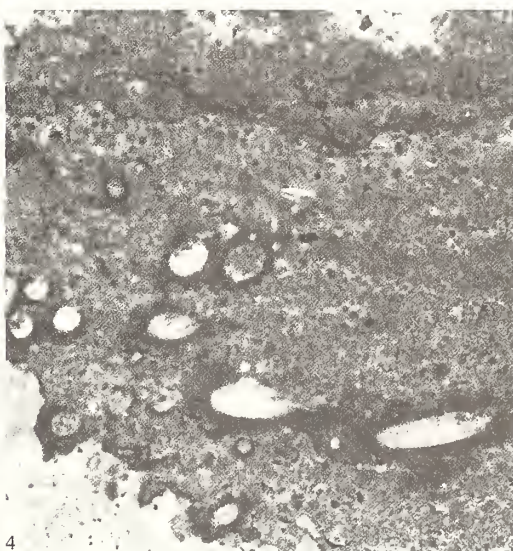
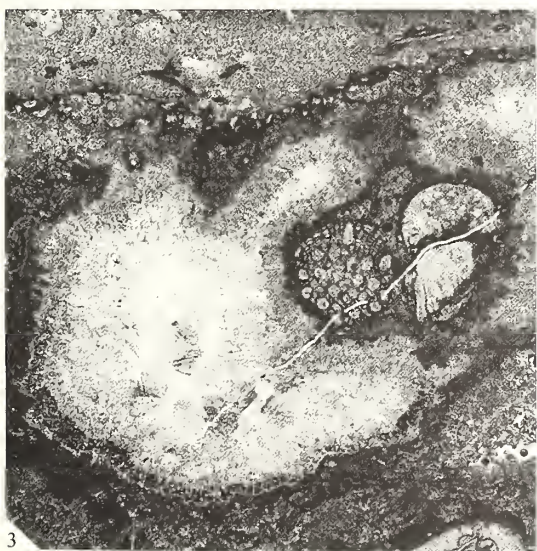
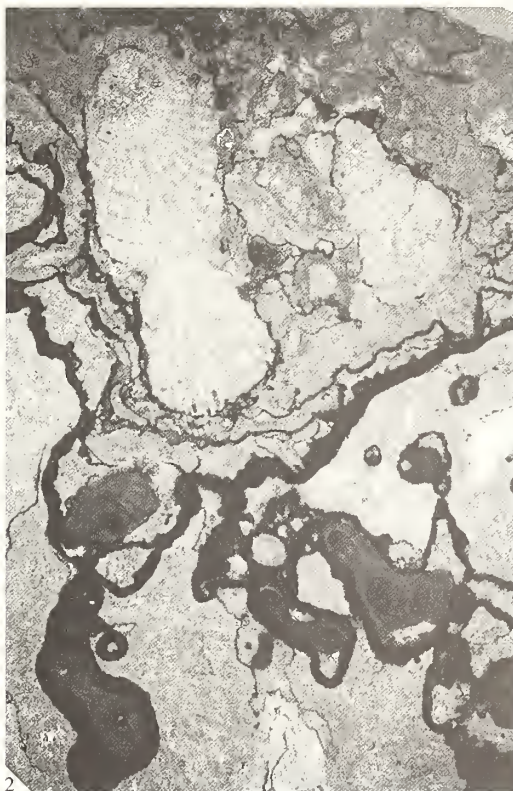


TABLE 1. Epibenthos identified within the frondose bryozoan-sponge community.

Open surface	Cryptos
Algae	Algae
<i>Archaeolithoporella</i>	<i>Archaeolithoporella</i>
Porifera	Porifera
Spinctozoans	Spinctozoans
<i>Guadalupia zitteliana</i>	<i>Girtycoelia</i> spp.
	<i>Guadalupia explanata</i>
	<i>Lemonea cylindrica</i>
	<i>Amblysiphonella</i> spp.
	<i>Cystauletes</i> spp.
	<i>Cystothalamia</i> sp.
	Hexactinellida
	?
	Cnidaria
	Rugosa
	<i>Lopophyllidium</i> ? sp.
Bryozoa	Bryozoa
<i>Acanthocladia</i> spp.	<i>Girtypora</i> sp.
<i>Fenestella</i> spp.	<i>Fistulipora</i> sp. 1
cf. <i>Polypora</i> sp.	<i>Fistulipora</i> sp. 2
<i>Goniocladia</i> sp.	<i>Fistulipora</i> sp. 3
	<i>Acanthodema</i> sp.
	Echinodermata
	Crinoidea
	?
Problematica	Problematica
<i>Tubiphytes</i>	<i>Tubiphytes</i>
	Unidentified massive encruster
	<i>Microborers</i>

These platy sponge communities are found only in bathymetrically shallow parts of the Capitan reef, where the sponges appear to have grown either perpendicular to the reef front out into ambient currents, or perhaps formed a series of domes or tunnels towards the top of the reef. These sponges formed the ceilings of huge open crypts up to 2 m in height and width (Text-fig. 7).

In McKittrick Canyon, the platy sponges were colonized by a cryptic community of small solitary spinctozoan sponges and small, nodular bryozoans (Pl. 4, figs 1, 4). Rare macroborings are found in the cryptos.

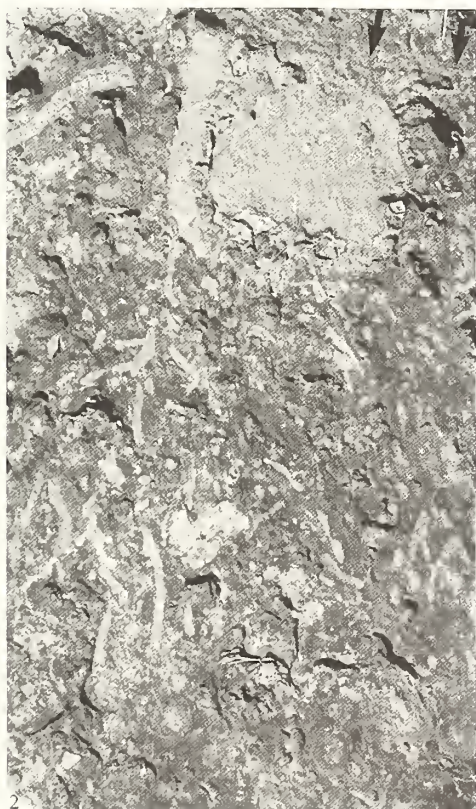
EXPLANATION OF PLATE 3

Platy sponge community

Fig. 1. Large individual of branching *Lemonea* sp. attached to the undersurface of *Gigantospongia discoforma*. Note attached crinoid stem (C) and bryozoan (B); $\times 0.67$.

Fig. 2. Extensive cavity ceiling formed by *Gigantospongia discoforma* (arrowed) supporting an extensive cryptos, including a branching individual of *Lemonea* sp. (left) and the compound *Guadalupia explanata* (right); $\times 0.2$.

Fig. 3. Detail of cryptos under *Gigantospongia discoforma*, including large sponge (S) and many bryozoans (B). Note encrustation of *Archaeolithoporella* on upper surface of *G. discoforma* and around the cryptos. Remaining cavity is filled with cement botryoids (I); $\times 0.67$.





TEXT-FIG. 7. Tracing of weathered surface approximately perpendicular to horizontal showing the development of large cavities and cryptic communities under the large platy inozoan sponges *Gigantospongia discoforma*, Walnut Canyon, Whites City, Upper Capitan Limestone. Inset is enlarged in Text-figure 8.

At Walnut Canyon, the undersurfaces of the platy sponges were colonized by a diverse cryptic community (Table 2) dominated by large sphinctozoan sponges (Text-figs 7–8; Pl. 3; Pl. 4, fig. 2). Compound sphinctozoans (e.g. *Lemonea conica*) grew up to 0.25 m in diameter (Pl. 3, fig. 2; Pl. 4,

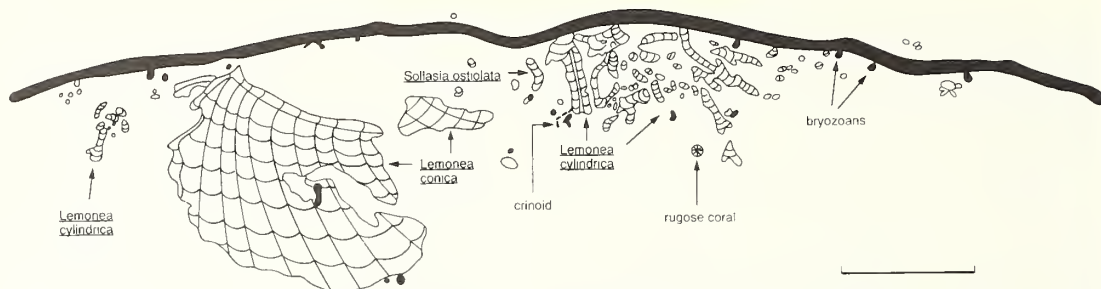
TABLE 2. Epibenthos identified within the platy sponge community.

Open surface	Cryptos
Algae	Algae
<i>Archaeolithoporella</i>	<i>Archaeolithoporella</i>
<i>Renalcis</i> ?	<i>Renalcis</i> ?
Porifera	Porifera
Sphinctozoans	Sphinctozoans
<i>Guadalupia explanata</i>	<i>Girtycoelia</i> spp.
	<i>Guadalupia explanata</i>
	<i>Lemonea cylindrica</i>
	<i>Lemonea conica</i>
Inozoans	<i>Lemonea polysiphonata</i>
<i>Gigantospongia discoforma</i>	<i>Lemonea</i> sp.
	<i>Parauvanella minima</i>
	<i>Discosiphonella mammosa</i>
	<i>Sollasia ostiolata</i>
	<i>Corymbospongia? permica</i>
	<i>Amblysiphonella</i> sp.
	Cnidaria
	Rugosa
	<i>Lopophyllidium?</i> sp.
	Byozoa
	<i>Acanthocladia guadalupensis</i>
	<i>Girtypora</i> sp.
	<i>Fistulipora</i> sp. 1
	<i>Fistulipora</i> sp. 2
	<i>Fistulipora</i> sp. 3
	Echinodermata
	Crinoidea
	?
Problematica	Problematica
<i>Tubiphytes</i>	<i>Tubiphytes</i>
	Macroboers
	Microborers

figs 2–3) and branching sphinctozoans (e.g. *Lemonea* sp.) up to 0.5 m long (Pl. 3, fig. 2). Branching acanthocladid bryozoan colonies up to 0.4 m long are also present. Small, nodular bryozoans are found attached either directly to the undersurfaces of the platy sponges (Text-fig. 8; Pl. 3, fig. 3), or nestled amongst the larger members of the cryptos together with small rugose corals and crinoids (Pl. 3, fig. 1; Text-fig. 8).

The upper surfaces of the platy sphinctozoans and cryptic community were thickly encrusted by generations of often intergrown foraminiferans, *Tubiphytes* and *Archaeolithoporella* (Pl. 3, fig. 3; Pl. 4, fig. 1). In Walnut Canyon, the community was patchily enveloped on both upper, open and lower cryptic surfaces by a poorly preserved greenish-grey micrite with a peloidal fabric resembling the calcified cyanobacteria *Renalcis* (Text-fig. 7; Pl. 4, fig. 3). This micrite is estimated to occupy less than 10 per cent. of the total reef fabric volume.

The considerable remaining pore space was infilled by small botryoids (7–20 mm radius) and intergrown *Archaeolithoporella*, followed by large brown botryoids (30–60 mm radius) alone. As in the frondose bryozoan-sponge community the botryoids nucleated on the crypt ceilings, walls and floors as well as from the projecting cryptos. Some minor geopetal infilling of coarse, bioclastic sediment is present (Text-fig. 7).



TEXT-FIG. 8. Tracing of weathered surface approximately perpendicular to horizontal, showing the development of an extensive cryptic community beneath a large platy individual of *Gigantospongia discoforma*. Upper Capitan Limestone, Whites City. Scale bar represents 0.1 m.

From these observations we infer the sequence of development of the platy sponge community to have been:

1. The growth of large, platy sponges which projected horizontally from the reef slope or formed tunnels towards the reef crest (Text-fig. 5B).
2. The undersurfaces of the largest platy sponges were colonized by an abundant cryptos dominated by large, pendent sphinctozoans (Table 2).
3. The upper surfaces of the sponges and cryptic epibenthic community were thickly encrusted by foraminifers, *Tubiphytes* and *Archaeolithoporella*.
4. The entire reef community was enveloped by a patchy growth of microbial micrite.
5. Cavity space was filled mainly by the syn-sedimentary intergrowth of aragonitic botryoids and *Archaeolithoporella*, and later by large botryoids alone.

TROPHIC RECONSTRUCTION

Text-figure 9 reconstructs the inferred trophic relationships between the community elements of the Capitan reef biota. Three broad trophic groups are distinguished: primary producers, primary consumers and predators.

Bacterial, phyto- and zooplankton are inferred to be present, but their relative importance is not known. Several supposed benthic primary producers are present: putative photosymbiotic fusulinid foraminiferans, calcified cyanobacteria (e.g. *Collenella*?) and possibly the putative red algae (e.g. *Archaeolithoporella*). These elements were volumetrically minor components of the biota with the exception of *Archaeolithoporella*, which was predominantly cryptic. The peloidal fabric of the encrusting micrite suggests a bacterial origin; the originators may have possessed photosynthetic

EXPLANATION OF PLATE 4

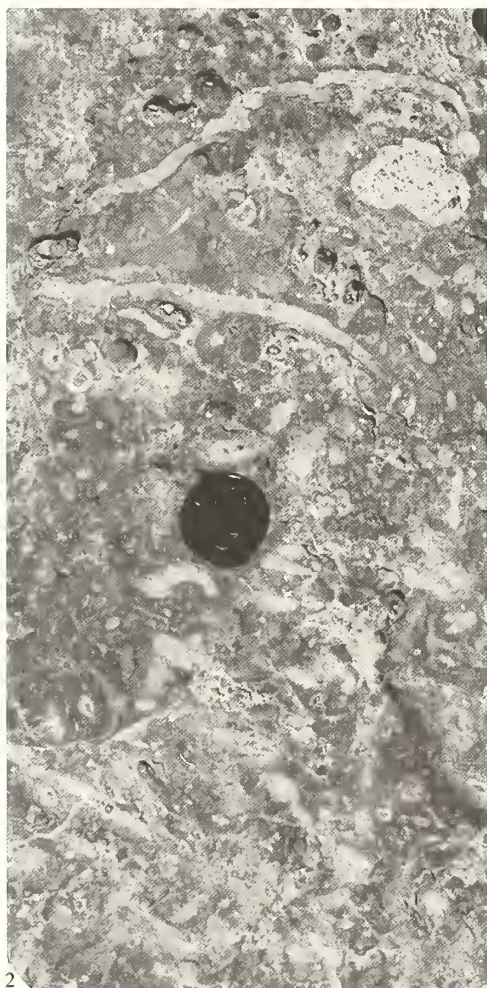
Platy sponge community

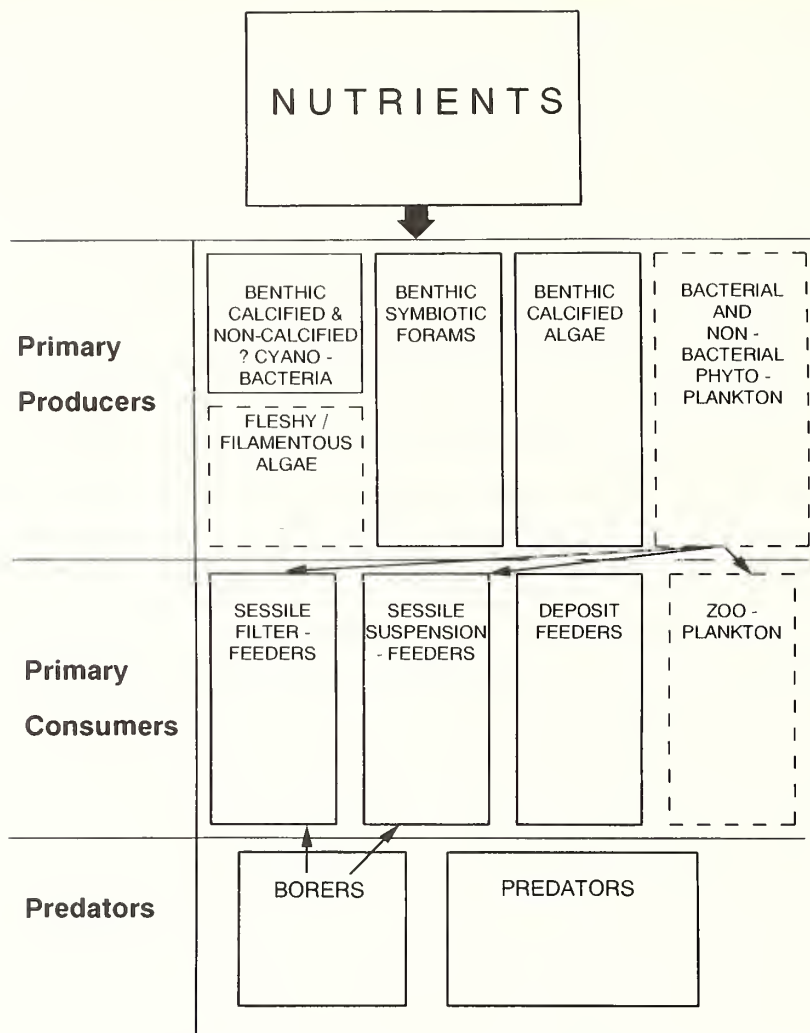
Fig. 1. Detail of fallen block in reef foreslope, McKittrick Canyon, inferred to be derived from the shallowest part of the Middle Capitan, showing the platy sphinctozoan *Guadalupia zitteliana* with cryptic bryozoans (arrowed), and *Archaeolithoporella* and intergrown botryoid encrustations on both upper and lower surfaces; $\times 1$.

Fig. 2. Etched surface of Upper Capitan Limestone from the mouth of Walnut Canyon, showing a tangential section through individuals of the cavity-forming platy sponge *Gigantospongia discoforma* and attendant solitary and branching cryptic sphinctozoans; lens cap diameter = 55 mm.

Fig. 3. Etched surface of Upper Capitan Limestone from the mouth of Walnut Canyon, showing large compound sphinctozoan *Lemonea conica* and other sphinctozoans attached to undersurface of *Gigantospongia discoforma*. Note patchy encrustation of ?microbial micrite (arrowed); $\times 0.25$.

Fig. 4. Fallen block in reef foreslope, McKittrick Canyon, showing stacking of the platy sphinctozoan *Guadalupia zitteliana*; lens cap diameter = 55 mm.





TEXT-FIG. 9. Trophic web reconstruction of the Permian Capitan reef ecosystem. Inferred categories are shown in dashed boxes.

capabilities. Fleshy and filamentous algae were most probably present, but were probably not volumetrically significant as few herbivores (with the possible exception of some gastropods) are recognized. There is no evidence to suggest therefore that benthic primary producers were trophically closely linked to primary consumers. The solitary and low-integration branching organization of most sphinctozoan sponges, their inferred internalized soft-tissue, as well as their cryptic habit indicates that they did not bear photosymbionts. Although the high-integration modular sponges such as *Gigantospongia discoforma* and *Guadalupia explanata* reached a very large size, there is also no evidence of either externalized soft tissue or the fast rates of growth or heavy calcification that might be expected in photosymbiotic forms.

The majority of the sessile Capitan reef metazoans were primary consuming heterotrophs. We distinguish between filter feeders capable of effective use of non-aggregated bacterial plankton and suspension feeders capable of capturing aggregates only. The most abundant element of the sessile community of primary consumers were sessile filter feeders; sphinctozoan, inozoan and spicular

sponges. The main diet of living sponges is planktonic bacteria (Reiswig 1974), and these bacteria also serve as the main food source for small cnidarians (Sorokin 1990) represented here by relatively uncommon rugosan and tabulate corals. Suspension feeders are represented by abundant brachiopods, bryozoans, crinoids and bivalves. Over 46 brachiopod species and 12 bryozoan species have been identified from the Capitan Limestone (Newell *et al.* 1953).

Inferred deposit feeders are represented by four species of gastropod and one species of trilobite. Other minor representatives of the fauna are scaphopods (one species), ammonoids (one species) and nautiloids (three species) (Newell *et al.* 1953). Scaphopods were probably slow-moving epifaunal detritophages, whilst the nautiloids and ammonoid may have been predators. This nekton may, however, have been part of the open water fauna of the Delaware Basin and not trophically closely linked to the reef. There is also rare evidence of macro- and microboring activity.

The Capitan community is thus notable for the proliferation of heterotrophic primary consumers, relatively little development of benthic calcified phototrophs and the absence of significant numbers of predators. This infers the presence of abundant suspended food matter presumably mainly in the form of plankton. Relatively high nutrient levels can thus be inferred to have been present in the Delaware Basin. Also, the waters were presumably devoid of much suspended sediment which would clog filter- and suspension-feeding mechanisms. Similar conclusions were reached by L. C. Babcock (1974), J. A. Babcock (1977) and Yurewicz (1977).

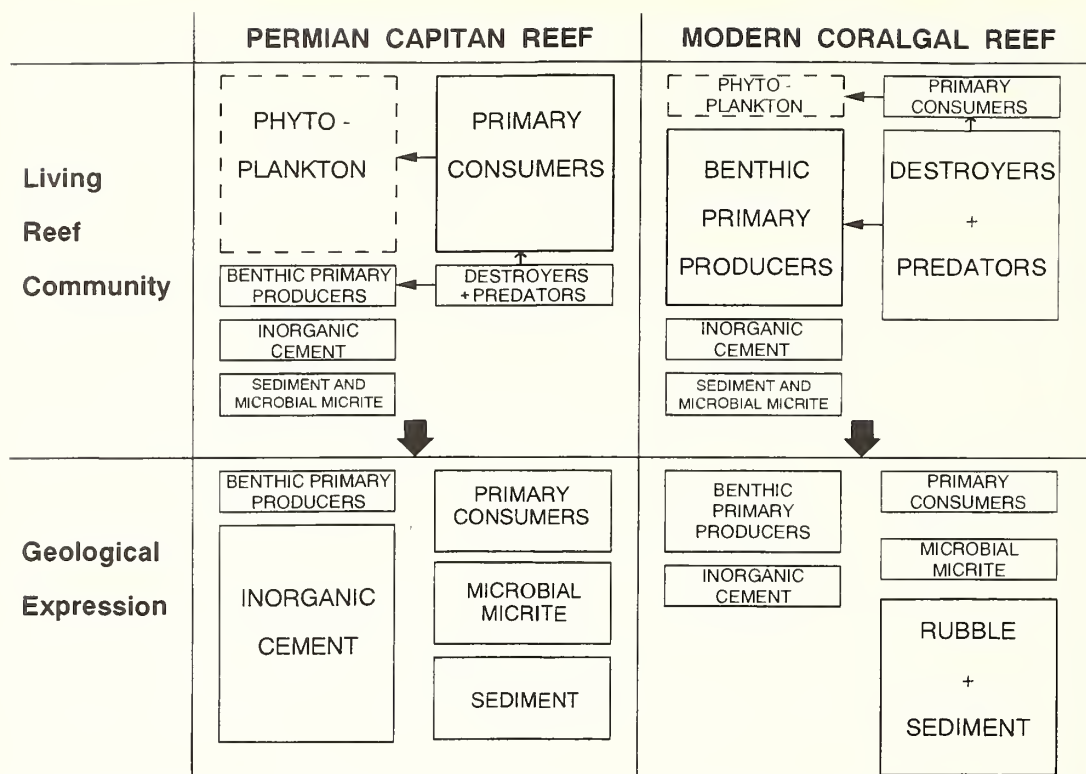
PRODUCTIVITY AND CARBONATE BUDGET

The Capitan Limestone ranges from 100 to 200 m thick and during the late Guadalupian interval (some 2.5 My) prograded 19 km basinwards on to the north central shelf. Estimates for the rate of the reef margin aggradation are 3.3–7.7 mm/yr during Lower Capitan time, and 1.1–2.6 mm/yr during the Middle and Upper Capitan (Garber *et al.* 1989: all figures neglect differential compaction). This yields an average rate of accumulation of 3–4 mm/yr giving the Capitan Limestone one of the most rapid accumulation rates of any known Phanerozoic carbonate platform (Garber *et al.* 1989). These rates compare well with modern reef accumulation, which is estimated to be an average of 3–4 mm/year (Buddemeier and Hopley 1988).

Such comparable rates of accumulation, however, mask substantially different relative contributions of organic and inorganic carbonate to the final reef fabric which result from profound differences in the ecology of the Permian Capitan reef compared with modern coralgal reefs. Modern coralgal reefs thrive in low nutrient seas and not surprisingly net planktonic primary productivity is estimated to be low: only one-tenth of the net benthic primary productivity (Grigg *et al.* 1984). Most productivity is derived from heavily calcified benthic coralline algae and photosymbiotic scleractinian corals.

The benthically dominated modern reef ecosystem is regulated by intense predation which controls higher trophic production. Modern reefs have exceptionally high levels of ecotrophic efficiency, with estimates indicating that between 50–85 per cent. of a species' annual production is consumed by predation or herbivory (Grigg *et al.* 1984). This high internal predation exists mainly between the heterotrophic benthos and reef fish. The effect of suitable habitat availability, which in turn determines the amount of photosynthetically active area, is also a major control in the gross primary production of modern reefs, and indeed may even be a limiting factor (Grigg *et al.* 1984; S. V. Smith 1981). Were similar constraints and controls also present during the Permian?

The trophic structure of the modern coralgal reef is profoundly different to that reconstructed for the Permian Capitan ecosystem (Text-fig. 10). Relatively few putative calcified photosynthesizers have been recognized in the Capitan: only a small proportion of overall productivity appears to have been present in the benthic photosynthetic community. Indeed, the calcified benthos is volumetrically dominated by heterotrophs, most of which were cryptic. To support such a rich community of primary consumers, it is necessary to infer high levels of plankton and therefore nutrients in the Delaware Basin. In addition, very few possible predators have been recognized and boring activity, although present, was extremely sparse.



TEXT-FIG. 10. Comparison of the relative volumetric contribution of different elements of the reef biota and associated inorganic sources of carbonate in the Permian Capitan and Recent corallgal reefs, in the living reef communities and in their geological expression. The Permian reef framework, whilst showing no evidence of a high degree of wave resistance, remained intact due to the absence of any significant numbers of destroyers and predators. Original crypts were thus preserved and became infilled with substantial volumes of inorganic cement. In contrast, the abundant predators and destroyers on modern corallgal reefs rapidly reduce the framework to mainly rubble and sediment.

The abundant herbivores and predators not only serve to regulate the trophic structure of modern corallgal reefs, but also rapidly reduce the otherwise robust framework to between 40–90 per cent. rubble and sediment (Hubbard 1989) by boring, rasping, etching and excavating activity. Otherwise intact framebuilders as well as reef rubble are commonly riddled extensively with borings such that the original reef-building framework is often totally obliterated (Macintyre 1977). Yet many of the abundant herbivorous, predatory and destructive elements did not appear in quantity until the mid-Mesozoic onwards – a radiation event known as the Mesozoic Marine Revolution (Vermeij 1977, 1987). In particular, the major groups of herbivorous and predatory fish on modern reefs did not appear until the Eocene.

We therefore suggest that the apparently fragile, but cavernous Permian reef framework, showed no evidence of physical destruction and hence substantial wave resistance, and remained intact largely due to the absence of significant numbers of predators and destroyers in the ecosystem. Original crypts were thus preserved firstly by encrustation (calcified encrusters and microbial micrite) and possibly pervasive microscopic cementation, and later by extensive infilling of crypts by inorganic cement. In contrast to modern reefs, where the overwhelming bulk of carbonate is organically derived and photosynthetically boosted (Barnes and Chalker 1990), a substantial

proportion of Capitan reef carbonate is thus contributed by inorganic cement processes (Text-fig. 10).

We conclude that before the Mesozoic Marine Revolution relatively fragile reefs could be preserved in areas where intense syndimentary cementation processes were active – in moderate- to high-energy environments with high rates of flushing. We therefore must consider Palaeozoic reef frameworks in a new light – the presence of either an intact fossil reef framework or similar rates of carbonate accumulation cannot infer that a fossil community grew under the same conditions as do modern reefs.

DISCUSSION

Differentiation of the biota

Reefs have been strongly differentiated into distinctive open surface and cryptic communities since their inception, although the identification of cryptic communities is frequently overlooked in palaeoecological analyses. Where studied, it has been shown that fossil reef crypts have often housed a substantial proportion of overall biodiversity (e.g. Kobluk 1988; Wood *et al.* 1993; Zhuravlev and Wood 1995). In modern corallgal reefs, open surface communities are dominated by phototrophic organisms – mainly coralline algae together with photosymbiotic metazoans. In contrast, filter and suspension-feeding organisms predominate in cryptic niches (Jackson and Buss 1975; Jackson 1977; Jackson and Winston 1982; Choi and Ginsburg 1983; Choi 1984). Encrusting sponges and bryozoans are abundant as they appear to be the best overgrowth competitors (Jackson and Winston 1982), but solitary organisms, such as serpulids, foraminiferans and brachiopods, are also conspicuous elements, even though they occupy little space (Jackson 1977).

Crypts provide niches well protected from direct exposure to local environmental pressures, such as wave scour, intense irradiation and predation. Unoccupied substratum is rare in crypts and overgrowths are frequent, suggesting that like the open surface, competition for space is intense. Nutrient supply and oxygen availability (provided by sufficient water flow) are critically important to modern cryptic communities (Kobluk and James 1979).

The two new Capitan reef communities here described represent a substantial proportion of the total discernible reef fabric in the Middle and Upper Capitan Limestone. Both communities display a previously unrecognized marked differentiation of the sessile calcified epibenthos into distinct open surface and cryptic communities (see Tables 1–2). Indeed, most of the overall diversity of the skeletal epibenthos of the Capitan reef was housed within the cryptos and, remarkably, most of the cryptic metazoans identified were obligate cryptobionts. Micrite-producing microbial communities appear to have been equally abundant on both the open and cryptic surfaces of the platy sponge community, but *Archaeolithoporella* grew predominately within crypts in both communities. Although sediment fills within crypts commonly contain abundant bioclastic debris (such as trilobite segments) as well as whole fossils (e.g. brachiopods and gastropods), we have not been able to exclude current sorting as a mechanism for the enrichment of these vagile organisms within crypts, and have therefore excluded them from our analyses.

The Capitan reef therefore differs from many described fossil reef ecologies in that most of the skeletal epibenthos was composed of obligate cryptobionts. This deserves explanation. Either ambient current energies were too high to favour the growth and/or preservation of these organisms on the exposed open surfaces, or these surfaces were covered by competitively superior, encrusting soft-bodied epibenthos. Because there is little evidence of significant numbers of herbivores in the Capitan ecosystem, this open surface community is unlikely to have been predominantly algal. Likewise, the absence of abundant spicules within crypt infill suggests that sponges did not form a substantial part of any soft-bodied community.

There is ample evidence that competition of cryptic surfaces in the Capitan was intense, as numerous examples of multiple encrustation and chains of several individuals have been observed (Pl. 2, fig. 1; Pl. 3, figs 1, 3). As on modern reefs, hard substrate was apparently at a considerable premium. In the Recent, solitary organisms tend to be poor space competitors on hard substrates as

they generally have small areas of attachment and lack specific competition mechanisms (Jackson 1977, 1985). Many solitary organisms do commonly occur, however, in modern cryptic habitats (Jackson 1977).

In both modern and fossil reef crypts, the size of cryptobionts appears to be related to the size of the crypt and time available for colonization (Zhuravlev and Wood 1995). The two cryptic populations in the frondose bryozoans-sponge and platy sponge communities are not only notably systematically different (see Tables 1–2), but differ also in terms of individual size and functional morphology. The cryptic sphinctozoans found in the frondose bryozoan community tend to be relatively small, solitary forms (usually 50–100 mm long), whilst those in the huge crypts of the platy sponge community display modular organizations (branching uniserial and compound multiserial) with individuals sometimes reaching 0.5 m in length. The vast majority of cryptobionts, however, including the multiserial sphinctozoans, bear notably small attachment sites (e.g. Pl. 1, figs 1, 3; Pl. 2, fig. 2; Pl. 3, fig. 2).

The ratio of modular to solitary species is proposed to be a function of substrate longevity (Jackson 1985) and indeed studies on community development in modern reefal crypts demonstrate that over time an ecological succession takes place from solitary to modular encrusting organisms (e.g. Choi 1984). The distribution of these different morphologies in the two described Capitan cryptic communities might therefore reflect this dynamic, but the expected succession from solitary to modular organizations is not observed in the large platy sponge community where it might be predicted. Surface area and volume were clearly variable in the Capitan crypts, and were determined by the size of the individual framebuilders. Indeed framebuilders not only determined the size of the crypts, but also the length of time the crypts were available for colonization: the large, relatively stable and presumably long-lived large platy inozoan sponges display noticeably larger cryptobionts than those inhabiting crypts formed under the smaller, more fragile frondose bryozoans. The larger average size of the botryoid cements within the crypts formed by the platy sponges also suggests that these crypts remained open for longer. That this community appears to have grown in more shallow, and probably more agitated waters may also be significant.

Interestingly, modern cryptic surfaces are dominated by multiple encrustations which are essentially two-dimensional (Jackson 1985). This is in stark contrast to the highly pendent and three-dimensional character of the Capitan reef crypts. Modern solitary organisms appear to be more dependent upon disturbance processes to provide suitable sites for settlement and growth than modular encrusting organisms, presumably because they are poorer competitors for space. Their generally small size, rapid growth rates and short generation times favour generalist, opportunist, or fugitive life strategies (Jackson 1977). Relatively few calcified multiserial encrusting organisms, however, were present in the late Palaeozoic compared with the mid-Palaeozoic, Mesozoic and Recent (Taylor 1990). In the absence of more efficient space competitors therefore, we might expect a greater dominance of pendent, solitary, calcified metazoans in the crypts during the Late Permian.

Large cryptic niches such as caves, grottoes and crevices have long held a celebrated status as refuges for faunas of an ancient caste. Modern reefal caves house putative relict communities of Mesozoic reef-building calcified demosponges ('sclerosponges') including sphinctozoans, and thecidian brachiopods (Jackson *et al.* 1971). Chambered sponges appear to have commonly inhabited a cryptic niche through the Palaeozoic (Wood *et al.* 1994; Zhuravlev and Wood 1995). Chambered archaeocyath sponges were common cryptobionts in Lower Cambrian reefs, as were Ordovician sphinctozoans from Koryakia, Russia and Silurian aphrosalpingids from Alaska and the Urals. Several groups of Palaeozoic chambered calcified sponges, previously interpreted as erect reef framebuilders, may in fact have been preferential crypt dwellers (Wood *et al.* 1994). Chambered calcified sponges exhibit varied morphologies, but most have small attachment sites. Such organizations conferred better competitive abilities within crypts than on open surfaces, where they would have been outcompeted by modular, encrusting organisms with an ability both to cover and occupy new substrate rapidly.

Importance of bryozoans in ancient reefs

The framebuilding importance of frondose bryozoans in the Capitan reef represents a radical departure from the established ecology. Modern bryozoans flourish principally between 10–80 m depth in oxygenated waters of normal salinity, clarity and moderate agitation, and in temperatures between 20–28 °C. Bryozoans in some Palaeozoic reefs constructed a semi-rigid lattice which created a framework for the settlement of other sessile, dwelling organisms (Cuffey 1974, 1977; Zimmerman and Cuffey 1987). Bryozoans also performed complementary roles of sediment baffling and trapping by encrusting or binding.

Bryozoans, especially fenestellids, have been described as major framebuilders in a number of reefs, e.g. the Mississippian of south-western USA (Pray 1958), the Dinantian of Ireland (Philcox 1971) and the Upper Permian reef of north-eastern England (D. B. Smith 1981a, 1981b). Bryozoans also played a supportive role in some Silurian reefs: Scoffin (1971, 1974) noted that the framework of Wenlock reefs in Shropshire consists mainly of bryozoans encrusted by stromatolites and partially infilled by micrite internal sediment. In some areas, fenestellid bryozoans formed the roofs of small cavities (1974: see fig. 4, p. 570).

Many Permian reefs display abundant bryozoans, both frondose and erect branching pinnate forms. Schwarzhacher (1961) serially sectioned reef limestone from the Lower Carboniferous of Ireland and demonstrated the presence of a growth lattice of fenestellid fronds, although he found no evidence for interconnections between colonies. Small bryozoan frame-thicket bioherms grew in deep waters, especially during the late early Permian and latest mid Permian, along the southern margin of the Delaware Basin (Zimmerman and Cuffey 1987). Etched material from the Glass Mountains reveals silicified bryozoan frameworks. Here, small bioherms consist of fenestrate and pinnate (most notably *Acanthocladia* spp.) zoari attached and intertwined, thereby creating a scaffolding with some structural rigidity (Zimmerman and Cuffey 1987). Calcified sponges, as well as brachiopods and fistuliporids, dwelt within the framework. Likewise, one of the dominant framebuilders in the Upper Permian reef of north-eastern England is also a species of *Acanthocladia* (D. B. Smith 1981a, 1981b). Babcock *et al.* (1977, p. 29) also illustrated frondose 'fenestellid' bryozoans from the Middle Capitan Limestone, McKittrick Canyon, creating what were interpreted as depositional shelters.

The apparent fragility of frondose bryozoans may be misleading in that their many fenestrule openings permitted water flow through the colony such that they could withstand quite strong currents (D. B. Smith 1981a). Frondose colonies also produced secondary thickening and were capable of lateral fusion and connection. McKinney and Gault (1980) deduced that most fenestellids lived in moderately energetic to relatively quiet waters, either near or below normal wavebase or in sheltered localities. Those with lyre-like growth morphologies could withstand more vigorous unidirectional currents. Indeed Elias and Condra (1957) considered that a conjoined lattice of fenestellids would be able to withstand turbulence when stiffened by a partial filling or coating of submarine cement or micrite.

Bryozoans predominantly inhabited open reef surfaces during the Palaeozoic (Cuffey 1974) but today they are more common in crypts (Kobluk *et al.* 1988). It has been suggested that they became predominantly cryptic during the Cenozoic (Cuffey 1974). Available evidence from calcified sponge groups, however, indicates that these modern cryptobionts are not displaced former open surface dwellers, but probably represent the remnants of communities which have always occupied cryptic niches. The evolution of light-dependency in scleractinian corals may have prompted the demise of open surface dwellers and restricted many calcified heterotrophs to the cryptos (Wood 1995).

Importance of microbial micrite and cement precipitation

Post-mortem microbial encrustation was clearly of considerable importance in the Capitan reef, especially in the frondose bryozoan-sponge community, in that it imparted considerable rigidity to an otherwise relatively fragile framework. Deposits of microbial micrite have been found extensively

in modern cryptic reef environments (e.g. Land and Moore 1980; Reitner and Neuweiler 1995). These studies suggest that the major control on micrite formation is the presence of Ca-binding organic matter. This has been found to often have its origin in decaying organisms, especially sponges and microbes. Crystal nucleation also requires increased carbonate alkalinity, which may be controlled by sulphate reduction in anaerobic layers of stratified water bodies (Reitner and Neuweiler 1995).

Locally, up to 70 per cent. (this study) or 80 per cent. (Schmidt 1977) of the Capitan reef may be occupied by marine cement. A similar volume of aragonitic marine cement has been estimated to be present within the bryozoan framework of the Upper Permian Magnesium reef, north-eastern England (Hollingworth and Tucker 1987). Indeed, large quantities of precipitated carbonates are globally common in the late Permian.

The Late Permian was a time of global low-stand in sea-level, and many authors have suggested the Late Permian ocean to have been stratified, with anoxic bottom waters (e.g. Margaritz and Turner 1982; Erwin 1994). This is supported by the unusual enrichment of ^{13}C in Late Permian carbonates, including those from the Capitan reef (e.g. Garber *et al.* 1989; Margaritz *et al.* 1992). Moreover, an alkalinity pump has been inferred to have controlled the amount of carbonate ions in the upper water masses (Margaritz and Turner 1982). The Zechstein and Delaware basins were also partially isolated from the world ocean, and both are thought to have been stratified with well-developed anoxic bottom waters which underwent periodic overturn (e.g. Newell *et al.* 1953; D. B. Smith 1981a; L. C. Babcock 1977; Margaritz and Turner 1982). The Delaware basin was probably sufficiently restricted so as to be particularly sensitive to continental runoff (Margaritz *et al.* 1983). All these phenomena would have favoured the precipitation of carbonate salts at the margins of the basins, especially where there was considerable flushing (Grotzinger and Knoll 1995).

Depth of formation, ecological zonation and bathymetric profile

The Capitan reef is one of the steepest known ancient prograding carbonate shelf margins. Existing erosional slope angles are usually 20–40°, whilst strata immediately landward of the reef have dips of 5–15°. The seaward slope on these so-called 'fall-in' beds has been taken by some (Hurley 1989) to be largely depositional and hence used to provide a measure of water depth over the reef, assuming that the fall-in beds were deposited up to sea-level. Others (e.g. Smith 1973; Newell *et al.* 1955) concluded that the seaward dip of the Capitan as well as the fall-in beds was the result of syndepositional or post-depositional tilting.

To resolve these competing hypotheses, Saller (1996) measured the strike and dips of geopetal surfaces in the Middle Capitan reef, McKittrick Canyon. He noted that such geopetal structures have a consistent basinward dip of 11° at an average azimuth of 130° (S50° E), which indicated a post-depositional basinward tilting of the Capitan at an angle perpendicular to the depositional strike of the Capitan reef in the area (40°; N40° E). Fall-in beds have similar basinward dips to geopetals in the Capitan reef. Saller (1996) thus concluded that differential compaction may have tilted the Capitan reef and fall-in beds when dense lithified reef and shelf carbonates prograded over the highly compactable lower-slope and basinal carbonate muds. Hence much of the apparent dip of the fall-in beds and reef should not be viewed as depositional and cannot be used explicitly to determine the depth at which the Capitan Limestone formed. These results would suggest that the depositional slope of the Capitan reef was in fact usually in the order of approximately 10–30°.

The Middle Capitan reef was dominated by the frondose bryozoan-sponge community, except for the uppermost 10 m of the reef. This community is also noted 13 m below the uppermost exposure of Upper Capitan Limestone at Walnut Canyon, marking the bathymetrically deepest community found in the Upper Capitan. The frondose forms which constructed the framework of the Middle Capitan show considerable secondary thickening and were capable of lateral fusion and connection. Although frondose bryozoan debris is noted in the Capitan reef, most of the bryozoan fronds are

intact. We consider that such a latticework would be able to withstand moderate turbulence, especially when stiffened by a partial filling or coating of submarine cement or micrite and further biological and microbial encrustation.

The Capitan reef is notable for the lack of zonation except in the bathymetrically most shallow parts. In modern corallgal reefs, well defined zones dominated by different scleractinian morphologies are present down to considerable depths on the reef front. Response to light availability, as well as wave energy, temperature and sediment input, is responsible for this zonation (Chappell 1980). Such a benthic phototrophic response has been recognized in only the most shallow parts of the Capitan reef: isolated colonies of the putative algae *Collenella* in the uppermost 10 m of Middle Capitan at McKittrick Canyon, branching *Tubiphytes* in the uppermost 5 m of Upper Capitan at Walnut Canyon and *Eugonophyllum* 13–10 m below the uppermost exposure at Walnut Canyon. This perhaps suggests that the remainder of the reef did not occupy the euphotic zone. Interestingly, D. B. Smith (1981a) also noted that the middle portions of the Upper Permian Magnesium reef, north-eastern England are characterized by an increase in the proportion of algae at the expense of bryozoans which were dominant in the earlier, possibly bathymetrically deeper, stages of reef growth. Modern reefs, being phototrophic, are restricted to the euphotic zone, and usually extend no deeper than 100 m. In contrast, the Capitan reef is thought to have reached some 150 m (Bebout and Kerans 1993).

The platy sponge community is restricted to bathymetrically shallow parts of the reef. In the Middle Capitan Limestone at McKittrick Canyon it occurs with *Collenella* towards the top of the reef. At Walnut Canyon, it forms a discrete horizon below the most shallow zone occupied by the *Tubiphytes*-sponge community. It appears to represent the lower part of the reef crest or the growing edge of the reef front itself.

The increased importance of putative algae in the Upper Capitan may indicate progressively more shallow growth of the reef. Alternatively, the uppermost parts of the Middle Capitan reef may not be preserved. The post-mortem microbial and inorganic lithifying processes acting upon the reef community were capable of forming a rigid structure, which, if growing in shallow waters, would have been capable of modifying the surrounding environment. Detailed study of the reef to shelf transition demonstrates that the reef did indeed modify the sedimentary processes that took place in its lee, and in so doing controlled sedimentation across the shelf (BLK, pers. obs).

SUMMARY

The Permian Capitan reef ecosystem was a highly differentiated community, where most of the sessile calcified epibenthic diversity was housed within the cryptos. Moreover, most members of the cryptos were obligate cryptobionts. Sponges in particular were markedly differentiated into both systematically and ecologically distinctive open surface and cryptic communities. Whilst open surface framebuilders were predominantly platy, multiserial forms, the cryptobionts, were rapidly establishing organisms with small attachment sites and solitary, branching and compound organizations. There is evidence of a soft-bodied cryptos and of intense competition for space, as cryptobionts commonly form multiple overgrowths and chains of individuals.

Cryptic habitats offered an alternative habitat of reduced environmental stress. However, unlike modern reefs, irradiation and predation were not important controls in the Capitan reef ecosystem. Except for microborings and rare macroboring, no evidence of biological destruction on the calcified benthos has been noted and very few predators have been recognized in the community. Benthic phototrophism was responsible for zonation only in the bathymetrically most shallow parts of the reef.

Unlike modern phototrophic corallgal reefs, the Capitan was a predominantly heterotrophic ecosystem, supported by inferred high levels of primary producing plankton in the Delaware Basin. Many workers (e.g. James 1983; Fagerstrom 1987; Kobluk 1988) have commented that truly cavernous, large-scale cavity systems did not appear in reefs until the appearance of large

TABLE 3. Comparison of the ecological characteristics of the Permian Capitan Reef and modern coralgal reefs. References: 1: Hubbard (1989); 2: James (1983); 3: Kirkland *et al.* (1993).

	Permian Capitan reef	Recent coralgal reefs
Major framebuilders	Heterotrophs: fenestellid bryozoans + platy calcified sponges	Mixotrophs, phototrophs: scleractinian corals + coralline algae
Volume occupied by organic framework in living reef (per cent.)	< 10	> 50
Volume occupied by inorganic framework in geological reef (per cent.)	> 40	< 10
Intact framework in geological reef (per cent.)	Up to 100	10–60 (1)
Wave energy	Low–medium	High
Destroyers and predators	Rare	Abundant
Zonation	Minimal	Marked
Maximum depth of reef front	Up to 150 m (3)	Up to 100 m (2)

phototrophic scleractinian corals in the Mesozoic. The Capitan reef, however, was a highly cavernous system, with large cavities up to 2 m in diameter in shallow parts.

Many studies of fossil reef communities have overemphasized the importance of massive framebuilders: the Capitan reef formed in their absence and its sustained growth and preservation was due to post-mortem microbial encrustation and extensive early cementation. Microbial encrustation was especially important in the frondose bryozoan-sponge community, where it imparted considerable rigidity to an otherwise fragile framework. Without such processes, the reef would probably have evolved as a bioclastic bank. In addition, the cavernous Permian reef framework remained intact due to the absence of significant numbers of destroyers in the ecosystem and to its inferred growth below the turbulent zone. As a result, in contrast to modern reefs where the overwhelming bulk of carbonate is organically derived, a substantial proportion (up to 70 per cent.) of Capitan reef carbonate (as exposed) is contributed by inorganic cement. Table 3 summarizes the ecological differences between the Permian Capitan and modern coralgal reefs.

Several groups of Palaeozoic chambered calcified sponges, previously interpreted as erect reef framebuilders, may in fact have been preferential crypt dwellers (Wood *et al.* 1994; Zhuravlev and Wood 1995). Such organizations, with their small attachment sites, may have been better competitors within crypts than on open surfaces, where they would have been outcompeted by high-integration, encrusting organisms with an ability to cover and occupy new substrate rapidly.

The ecological interpretations presented here represent a radical departure from the established descriptions. They are not, however, intended to present a complete review of the ecology of the Capitan reef: rather to offer a new frame of reference in which further observations can be placed.

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RHOMBOPHOLIS, A PROLACERTIFORM REPTILE FROM THE MIDDLE TRIASSIC OF ENGLAND

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ABSTRACT. The first prolacertiform from the British Isles is described. The type specimen of *Rhombopholis scutulata*, from the Middle Triassic of Warwick, was originally described as a temnospondyl amphibian. The specimen contains bones belonging to a large and a small prolacertiform, both possibly of the same species, as well as scales of a palaeonisciform fish. Prolacertiform characters of the small individual include long and low cervical vertebral neural spines, horizontal neural spine tables on the cervical vertebrae, tall rectangular dorsal vertebral neural spines, and, in a specimen of the presumed larger individual, a strong preacetabular crest on the ilium. Other material of the prolacertiform is noted from Warwick and Bromsgrove. The material is inadequate for confident diagnosis, but it shows closest similarities with *Macrocnemus* from the Middle Triassic of continental Europe.

THE Middle Triassic of England has yielded a diverse fauna of fishes, amphibians, and reptiles, together with arthropods and other invertebrates, and plants from a number of localities (Walker 1969; Benton 1990; Milner *et al.* 1990; Benton *et al.* 1994). One of the most prolific units has been the Bromsgrove Sandstone Formation of the Warwick area, and of Bromsgrove, both in the West Midlands of England (Text-fig. 1). The Bromsgrove Sandstone Formation of Warwick has produced a fauna of three amphibian taxa, a stenotosaurine temnospondyl, a cyclotosaurine temnospondyl, and *Mastodonsaurus* (Paton 1974; Milner *et al.* 1990), and two or three reptiles, the rhynchosaur *Rhynchosaurus brodiei* (Benton 1990), the rauisuchian *Bromsgroveia walkeri* (Galton 1985; Benton and Gower in press), and some other possible archosaurs (Walker 1969; Benton and Gower in press). The Bromsgrove Sandstone Formation of Bromsgrove has yielded a similar tetrapod fauna (Walker 1969; Paton 1974), as well as abundant plants (equisetaleans and conifers) and invertebrates and other vertebrates (annelids, bivalves, scorpions, branchiopods, a lungfish, and a perleidid bony fish; Wills 1910). The tetrapod-bearing horizons in both areas have been dated as Anisian (Warrington in Benton *et al.* 1994). Fuller details of the faunas may be found in Benton *et al.* (1994) and Benton and Spencer (1995).

One of the most unusual fossils from the Bromsgrove Sandstone Formation, *Rhombopholis scutulata* (Owen, 1842a), was interpreted by Owen (1841a, 1842a, 1842b) as a 'labyrinthodont' amphibian, an identification questioned by Miall (1874). Walker (1969) reinterpreted this specimen, and others from Warwick and Bromsgrove, as a prolacertiform reptile possibly related to *Macrocnemus*, a form well known from the Middle Triassic of northern Italy, Switzerland, Germany, and possibly Spain. *Rhombopholis scutulata* (Owen, 1842a) is the first-named prolacertiform, pre-dating *Tanytropheus* von Meyer, 1855 and *Protorosaurus* von Meyer, 1856. The purpose of this paper is to describe the English Middle Triassic prolacertiform specimens, including the type material of *Rhombopholis scutulata*, and to reconsider their identifications.

Repository abbreviations. BMNH, The Natural History Museum, London, formerly British Museum (Natural History); CAMSM, Sedgwick Museum, Department of Earth Sciences, Cambridge University; PIMUZ, Paläontologisches Institut und Museum der Universität, Zürich; WARMS, Warwickshire Museum, Warwick.



TEXT-FIG. 1. The Triassic of England: map showing the distribution of Triassic rocks, and the location of sites mentioned in the text.

MATERIALS

The specimens described here were collected from localities in and around Warwick and at Bromsgrove, the first in 1840. A.D.W. began work on this material in 1967, prepared specimens, and later published a review (Walker 1969). In the present paper, ADW produced Text-figures 4–8 and 10, and Plate 1, and MJB Text-figures 1–3 and 9; the remainder of the work has been carried out jointly. The material comprises:

1. WARMS Gz10, a small block containing 16 major bones (four vertebrae, five limb bones, seven other pieces) and numerous scales. From Leamington Old Quarry (?), collected by Dr G. Lloyd in summer 1840. Described by Owen in February 1841 (Anon. 1841a, 1841b; Owen 1841b, 1842a, p. 538, pl. 46, figs 1–5, 1842b, pp. 183, 188). Noted by Owen (1860, p. 194, 1866, p. 15), Miall (1874, p. 432), Allen (1909, p. 276), Walker (1969, p. 472), Paton (1974, p. 253), Benton (1990, p. 288), and Benton *et al.* (1994).
2. WARMS Gz21, proximal portion of a left femur. From Coton End Quarry, Warwick, collected by Dr G. Lloyd. Described by Owen (1842a, p. 533, pl. 45, figs 11–15, 1842b, p. 187) as the proximal end of a humerus of *Labyrinthodon pachygnathus*. Indicated as non-*Labyrinthodon* by Miall (1874, p. 431), and as cf. *Macrocnemus* by Walker (1969, p. 472).
3. WARMS Gz4714, a left ilium. From Coton End Quarry, Warwick, collected by J. W. Kirshaw, and donated in 1872. Noted as cf. *Macrocnemus* by Walker (1969, p. 472).
4. CAMSM G.343, a dorsal vertebra. From the Hilltop Quarries, Bromsgrove, collected by L. J. Wills. Indicated by Wills (1910, p. 264) as a ?rhynchosaur vertebra ('*Hyperodapedon gordonii*'), and reidentified by Walker (1969, p. 472) as cf. *Macrocnemus*.

The elements on WARMS Gz10 appear to comprise fish remains (the scales, and perhaps some bones) and at least two prolacertiform individuals, a small one and a large one, representing either two individuals of a single species, or two species. WARMS Gz21, 4717, and CAMSM G.343 match the large individual of WARMS Gz10 in size.

SYSTEMATIC PALAEOLOGY

Class REPTILIA Laurenti, 1768

Subclass DIAPSIDA Osborn, 1903

Infraclass NEODIAPSIDA Benton, 1983b

Division ARCHOSAUIROMORPHA von Huene, 1946

Order PROLACERTIFORMES Camp, 1945

Genus RHOMBOPHOLIS Owen, 1866

Rhombopholis scutulata (Owen, 1842a)

- 1841a *Inisopus* [sic] *scutulatus*; Anonymous, p. 2.
- 1841b *Anisopous scutulatus*; Anonymous, p. 4.
- 1841a *Labyriuthodon* [sic]; Owen, pp. 581, 582.
- 1842a *Labyriuthodon* (*Anisopus*) *scutulatus* Owen, p. 583, pl. 46, figs 1–5.
- 1842b *Labyriuthodon scutulatus* Owen; Owen, pp. 183, 188.
- 1854 *Labyriuthodon scutulatus* Owen; Morris, p. 350.
- 1859 *Labyriuthodon scutulatus*; Howell, p. 40.
- 1860 *Labyriuthodon scutulatus* Owen; Owen, p. 194.
- 1866 *Rhombopholis scutulata* Owen; Owen, vol. 1, p. 15.
- 1868 *Labyriuthodon scutulatus* Owen; Hull, pp. 6, 121.
- 1871 *Labyriuthodon scutulatus* Owen; Phillips, p. 97.
- 1874 not *Labyriuthodon*; Miall, p. 432.
- 1890 *Rhombopholis scutulata* Owen; Woodward and Sherborn, p. 207.
- 1909 *Rhombopholis scutulata* (Owen); Allen, p. 276.
- 1909 *Labyriuthodon* 'scutulatus' Owen; Horwood, p. 279.
- 1969 'Rhombopholis scutulata' Owen; Walker, p. 472.
- 1974 small lepidosaurian reptile; Paton, p. 253.
- 1990 cf. *Macrocnemus*; Benton, p. 288.

Lectotype. We specify the small reptile on WARMS Gz10 as the lectotype, since it is represented by more elements than the large individual, and these include the diagnostic vertebrae. The slab contains vertebrae, limb bones, and unidentifiable elements of at least two individuals, as well as scales of a palaeonisciform fish, possibly *Gyrolepis*. This is the only specimen described and named by Owen (1842a, p. 538; 1842b, pp. 183, 188) and the only specimen illustrated in various views by Owen (1842a, pl. 46, figs 1–5).

Type locality and horizon. Noted as 'Leamington' by Owen (1841a, 1842a, 1842b), and possibly Old Leamington Quarry (?SP 325666), a source of several finds of fossil tetrapods. An old label reading 'Leamington' is stuck to the side of the block. The source horizon is from about the middle of the Bromsgrove Sandstone Formation, which lies at the top of the Sherwood Sandstone Group, just below its contact with the Mercia Mudstone Group (Warrington *et al.* 1980). The age, obtained by correlation with laterally equivalent units which have been dated by miospores, is Anisian (lower Middle Triassic).

Distribution. Other postulated prolacertiform remains from England, which may or may not pertain to the same taxon as the type specimen of *Rhombopholis scutulata*, include specimens from Coton End Quarry, Warwick (SP 289655) and Hilltop Quarries, Bromsgrove (SO 948698), also from the Bromsgrove Sandstone Formation.

Status of the taxon. It is impossible to give a cladistic diagnosis of the genus *Rhombopholis*, and of the species *R. scutulata*, since the limited material offers no autapomorphies. The taxon is prolacertiform on the basis of the long, low neural spine on the postulated cervical vertebra '1' (Text-fig. 4), a synapomorphy of Prolacertiformes (Benton 1985; Evans 1988), and the ovoid neural spine tables, but there are no features that distinguish this taxon from other prolacertiforms. Further prolacertiform synapomorphies are seen in CAMSM G.343 (the square dorsal neural spine), and in WARMS Gz4714 (the marked preacetabular buttress).

The name *Rhombopholis scutulata* (Owen, 1842a) is retained as a metataxon, a taxon that may be distinct from all others, but which currently offers no autapomorphies for its definition (Gauthier 1986).

The type specimen

The lectotype of *Rhombopholis scutulata* (Owen, 1842a), WARMS Gz10 (Text-figs 2–3), was collected in the summer of 1840 by Dr G. Lloyd of Leamington, and sent to Richard Owen, who described it in an oral paper to the Geological Society of London on 24 February 1841. In an extended abstract of this paper, Owen (1841a, p. 581) stated that ‘at Leamington there was discovered a closely and irregularly aggregated group of bones manifestly belonging to the same skeleton, and including four vertebrae more or less complete, portions of ribs, a humerus, a femur, and the two tibiae, one end of a large flat bone, and several small dermal osseous scutae’. He further described (p. 582) the vertebrae as ‘batrachian’ and commented on the ribs and dermal scutes. No name is given to this form, although the report refers to ‘three species of *Labyrinthodon* [sic]’, but names only *Labyrinthodon leptognathus* and *L. pachygnathus*. However, the third species was named in newspaper reports (e.g. Anon. 1841a, 1841b): *Anisopous* was presumably used by Owen in his address, but not reproduced in the long account (Owen 1841a). The name *Anisopous* was also used informally by others at this time (e.g. letter from T. Ogier Ward to Owen, dated 26 October [1841], in which he assumes that the small slender *Rhynchosaurus articeps* Owen, 1842b from Grinshill, Shropshire is the same animal; Owen Correspondence, Coll. Sherborn, BMNH letter 114).

As a further confusion, Owen (1841b, pl. 62A, fig. 3) used the name *Anisodon gracilis* for a specimen from Leamington (?or Warwick) first illustrated by Murchison and Strickland (1840, pl. 29, fig. 9), and interpreted by Owen as an ungual phalanx of *Labyrinthodon* (see also Owen 1842a, p. 535). This proved to be part of a premaxilla of *Rhynchosaurus brodiei* Benton, 1990 (see p. 254, fig. 22a). Owen (1842a, p. 538, and explanation of pl. 46, figs 1–5) termed the present specimen *Labyrinthodon (Anisopus) scutulatus*, presumably intending *Anisopus* as a subgeneric name distinguishing this species from the larger forms with sculptured skull bones described earlier in his paper (*L. leptognathus* and *L. pachygnathus*). Owen did not use the name *Anisopus* in a further paper that he must have been writing at about the same time (Owen 1842b), the published account of his British Association address given in August 1841, and published in April 1842 (Torrens 1992): the present specimen is named simply *Labyrinthodon scutulatus*.

The name *Anisodon* is a *nomen dubium*, since it was not adequately characterized, and since it is unclear whether it refers to the rhynchosaur alone, or to other material as well, possibly including the present specimen. The name *Anisopus* could stand as valid for the specimen WARMS Gz10, although Owen subsequently abandoned it, perhaps because he found that it was multiply pre-occupied by usages before 1842 for genera of Diptera (Meigen 1803), Crustacea, and Coleoptera. Owen (1860, p. 193) did not use the name *Anisopus*, but repeated (p. 195) his earlier idea that the characters of *L. scutulatus* ‘might present differences of subgeneric value’ should more remains come to light. In another book, Owen (1866, vol. 1, p. 15) introduced the name *Rhombopholis* as one of two genera of Labyrinthodontia, the other being *Labyrinthodon*. He did not specify that the new name referred to *L. scutulatus*, but its meaning (‘rhomboid [scale-] bearer’), and his diagnosis of Labyrinthodontia, including the phrase ‘exoskeleton, in some, as small ganoid scales’ seems fairly conclusive. One clear feature of WARMS Gz10, referred to by Owen in establishing the species *L. scutulatus* (and the source of its specific name) is the association of the bones with numerous rhomboid ‘ganoid’ scales, interpreted by Owen as part of the integument of the ‘batrachian’, and here by us as a chance association with scales of the palaeonisciform fish *Gyrolepis*.

We can find no substantial later reference to *Rhombopholis*, except in reviews of the Bromsgrove Sandstone Formation fauna by Miall (1874), Walker (1969), Paton (1974), Benton (1990), and Benton *et al.* (1994). The genus name is listed by Woodward and Sherborn (1890, p. 207) as an amphibian, and by von Huene (1956, pp. 93–94), Shishkin (1964, pp. 95–96), and Romer (1966, p. 363) as a synonym of *Mastodonsaurus* (of which *Labyrinthodon* is also a synonym), but it is not noted by Carroll (1987).

DESCRIPTION OF WARMS Gz10

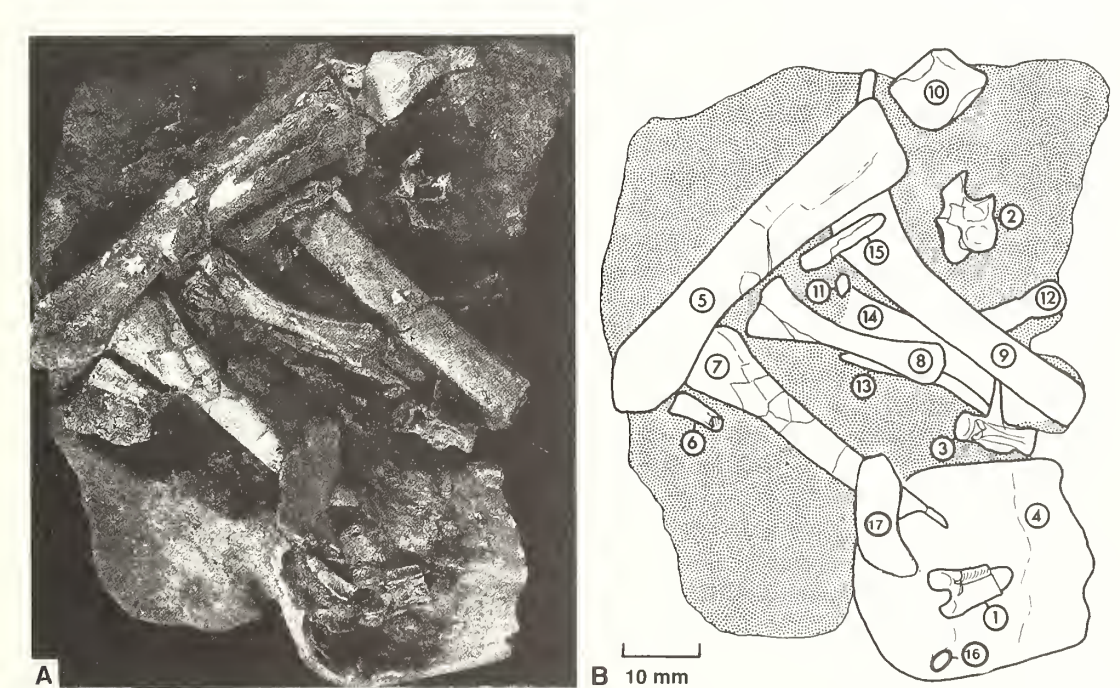
The elements represented in WARMS Gz10 are listed in Table 1, and shown in Text-figures 2–7. The elements numbered 1–3, 6, and possibly 7 and 17, belong to the small animal, elements 4–5, 8–9, and perhaps 10 belong to the large animal, and elements 11 and 16 are fish scales, elements 12–15 possibly fish bones. The material is described in that sequence.

The small animal (Text-figures 2–5)

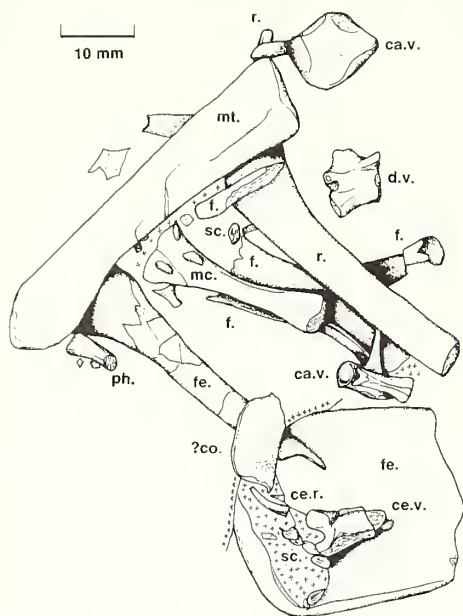
Middle or posterior cervical vertebra. This element (‘1’, Text-figs 2–4) is broken on the left side and at the back, and the anterior end is a little eroded. The centrum is slightly constricted in the middle, and the ventral margin

TABLE 1. The main elements represented in specimen WARMS Gz10, numbered arbitrarily, and summarizing Owen's (1842*a*, 1842*b*) identification, and the present interpretation. The specimen is illustrated in Text-figures 2–3, and the numbering scheme is reproduced in Text-figure 2*B*. The identity codes indicate our assignments of elements to the small prolacertiform (S), the large prolacertiform (L), or the fish (F).

Number	Owen's (1842 <i>a</i> , 1842 <i>b</i>) identification	Present identification	Identity code
1	vertebra	mid-cervical vertebra	S
2	vertebra	anterior dorsal vertebra	S
3	vertebra	caudal vertebra	S
4	?part of lower jaw	proximal end of right femur	L
5	tibia	metatarsal IV	L
6	?rib	phalanx	S
7	femur	?femur	?S
8	humerus	metacarpal II, III, or IV	L
9	tibia	large rib (passes below 5)	L
10	femur	partial caudal vertebra	?L
11	dermal scute	fish scale	F
12	?vertebra	?fish element	?F
13	?radius/ulna	?fish element	?F
14	?radius/ulna	?fish element	?F
15	?rib	?fish element	?F
16	dermal scute	fish scale	F
17	?	?coracoid	?S



TEXT-FIG. 2. The type specimen of *Rhombopholis scutulata* (WARMS Gz10). A, photograph showing the major elements. B, key to the photograph, showing the major elements and the arbitrary numbering scheme followed in the text.



TEXT-FIG. 3. The type specimen of *Rhombopholis scutulata* (WARMS Gz10). Drawing showing the major elements. Abbreviations: ca.v., caudal vertebra; ce.r., cervical rib; ce.v., cervical vertebra; ?co., possible coracoid; d.v., dorsal vertebra; f., fish bone; fe., femur; mc., metacarpal; mt., metatarsal; ph., phalanx; r., rib; sc., fish scale. Some identifications are tentative (see text).

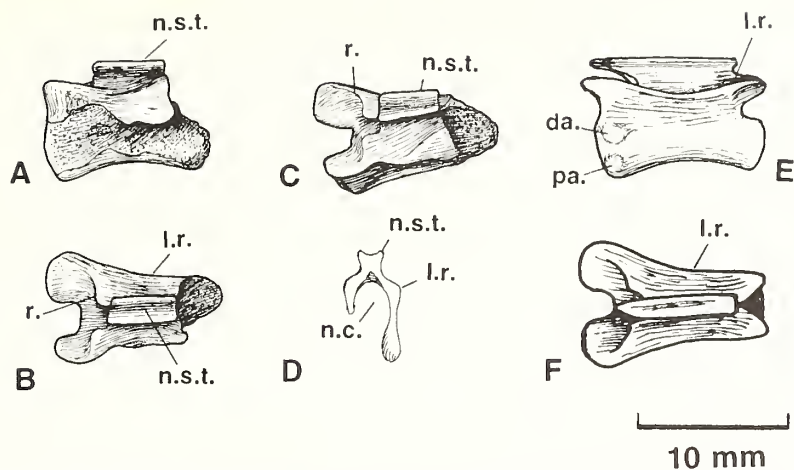
is rounded and without a keel. The right side of the centrum is preserved, but is difficult to observe because it is closely pressed against the large femur head ('4'); there appear to be two rib facets (diapophysis and parapophysis), lying at the anterior margin of the centrum (da., pa., Text-fig. 4E). The prezygapophyseal facets are broad, with a slightly squared outline, and they slope up and laterally at an angle of about 10° above horizontal. The prezygapophyses are linked by a horizontal shelf above the neural canal and in front of the anterior margin of the neural spine. Narrow ridges run from the neural spine to the postero-lateral margin of the prezygapophysis, and from the prezygapophysis to the postzygapophysis (r., l.r., Text-fig. 4B-C, E-F). The postzygapophyses on both sides are incomplete, and lie above a seemingly wide neural canal (n.c., Text-fig. 4D). The neural spine is low and long, and provided with an expanded, horizontal flat top.

This vertebra is similar to posterior cervicals of prolacertiforms, such as *Protorosaurus* (Seeley 1888), *Macrocnemus* (Peyer 1937, p. 98), and *Tanystropheus conspicuus* (von Huene 1908a, fig. 243), but not *T. longobardicus* (Wild 1973), because of the great elongation of cervical vertebrae in the last. The closest resemblance of this *Rhombopholis* vertebra is to cervical 6 or 7 of *Prolacerta* (Gow 1975, fig. 21; Colbert 1987, fig. 7), except that the neural spine in the latter is higher. The neural spine table in *Prolacerta* is nearly identical in dorsal view, as it is in *Malerisaurus* (Chatterjee 1980, fig. 8).

Anterior dorsal (? or posterior cervical) vertebra. This vertebra ('2', Text-figs 2-3, 5A-F) has been prepared in the round, and detached from the main block. It is perfectly preserved, except for some damage at the posterior end (Text-fig. 5F). The centrum is constricted in the middle, and passes into the neural arch without an evident suture. The centrum is broader than high, and has a deeply excavated anterior face. The parapophysis is probably represented by a roughened facet half-way down the anterior margin of the centrum (pa., Text-fig. 5D).

The neural canal is ovoid and twice as wide as high (Text-fig. 5A-B). The prezygapophyses are supported on broad pedestals, and diverge widely, sloping up laterally at an angle of about 20° above horizontal. The neural spine is low and capped by a table, as in the cervical vertebra '1'. This neural spine table has a shallow V-shaped cross section and bears a slightly rugose ornament on its upper surface (n.s.t., Text-fig. 5A-C). This table comes to a point, and projects anteriorly over the prezygapophyses. In front of the neural spine, a sharp ridge runs to the prezygapophysis (r., Text-fig. 5A-C). The prezygapophyseal pedestal expands laterally at its base to support the diapophysis (da., Text-fig. 5A-E). The postzygapophyses have facets sloping up laterally at an angle of about 20° , which connect directly to the neural spine table by mediodorsally running ridges on each side.

This specimen resembles the anteriormost dorsals of *Macrocnemus* (Peyer 1937) and *Tanystropheus* (Wild 1973, fig. 52). It resembles the presacral vertebra 10 of *Prolacerta* illustrated by Gow (1975, fig. 21), especially



TEXT-FIG. 4. The type specimen of *Rhombopholis scutulata* (WARMS Gz10). Cervical vertebra, element '1' of the 'small' individual, in: A, left lateral; B, dorsal; C, oblique dorso-lateral; D, posterior; E, restored left lateral; and F, restored dorsal views. Abbreviations: da., diapophysis; l.r., lateral ridge; n.c., neural canal; n.s.t., neural spine table; pa., parapophysis; r., ridge.

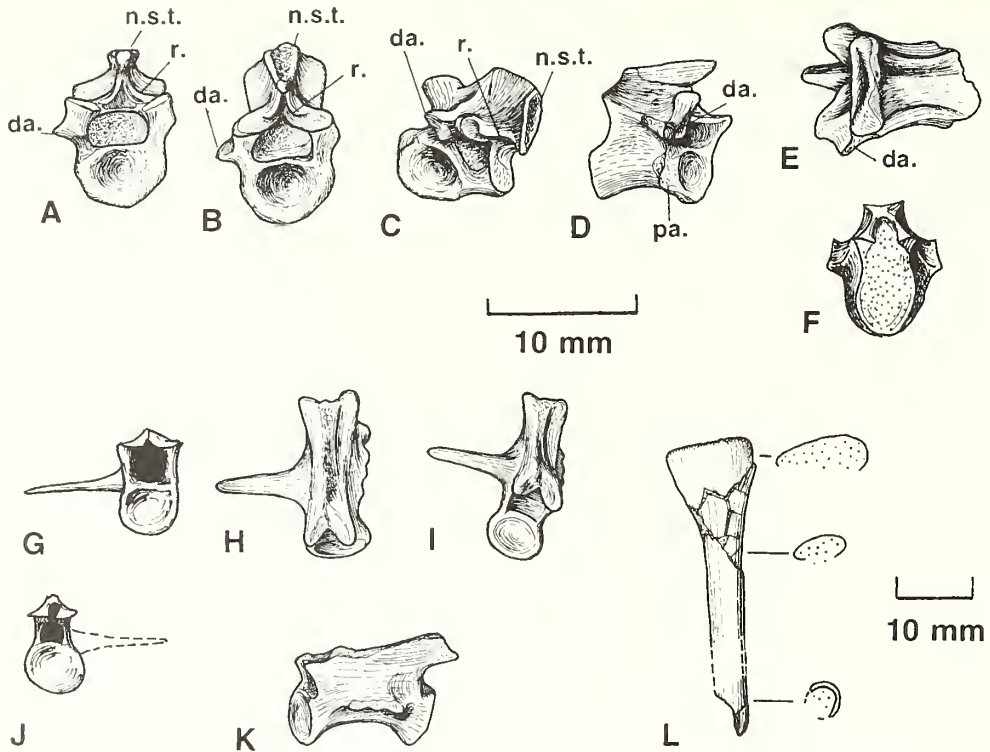
in anterior and posterior views, and also resembles the presacral 7 or 8 of *Malerisaurus* shown by Chatterjee (1980, fig. 8, 1986, fig. 5).

Anterior caudal vertebra. This vertebra ('3', Text-figs 2-3, 5G-K) is nearly complete, lacking only the transverse process on the left side and the neural spine, and having the right side partly obscured by matrix and by element '9'. The centrum is lower and narrower than in the other two vertebrae, and its ventral margin arches up. There is no ventral keel, but there is a bevelled surface for a chevron on the postero-ventral margin. The anterior and posterior faces of the centrum are more circular than those of the other two vertebrae, and they slope back at 10-20° from the vertical.

The neural arch is fused to the centrum without evident suture. The neural canal is bounded by slender vertical walls, and is broader than high in front, but seems more equidimensional behind. The small prezygapophyses slope up laterally at about 20° above horizontal, and they are supported on narrow pedestals on either side of the neural canal. A slender ridge runs back from the lateral margin of the prezygapophysis above the long, slender, horizontal transverse process. The length of the transverse process cannot be estimated since it passes below the large rib '9'. Below the transverse process is a deep longitudinal groove in the side of the centrum (Text-fig. 5K). The postzygapophyses join at the base of the neural spine only a short distance above their articular facets. The apparent great length of the transverse process is not excessive in comparison with *Macrocnemus* (Peyer 1937, pl. 63) and *Taustropheus antiquus* (Ortlam 1967, pl. 45, fig. 3).

Phalanx. The postulated phalanx ('6', Text-figs 2-3) is a short square-sided element lying close to long bone '5'. It is exposed apparently in ventral view, the uppermost face being flat and depressed below the raised edges. One end is seemingly unbroken and straight and appears to be deeply excavated, probably as a result of erosion of an unfinished cartilaginous portion. The element narrows symmetrically towards the other end, but this is damaged. A distal ligament pit is seen on the side closest to element '7' on the slab.

Femur. Element '7' (Text-figs 2-3, 5L), a possible femur, cannot be identified with certainty. It is a long bone, evidently rather thin-walled and more heavily cracked than all other elements on the slab. If it belonged to the large individual, it would have to be interpreted as a metapodial, but it seems too long and slender to be a metatarsal (cf. '5', Text-figs 2-3) and too long and robust to be a metacarpal (e.g. '8', Text-figs 2-3). The overall shape is like the femur of *Macrocnemus* (e.g. Peyer 1937, figs 27, 36, pls 55, 59-61). The present element is broadest at its (postulated) proximal end, and the expansion is asymmetrical with respect to the shaft. The proximal margin seems to be straight, and the widest expansion is presumably towards the anterior margin, making this a left femur, assuming that the exposed side is dorsal (it is convex up and displays no sign of an internal trochanter nor a concave intertrochanteric fossa). The shaft is relatively straight-sided (Text-fig. 5L),



TEXT-FIG. 5. The type specimen of *Rhombopholis scutulata* (WARMS Gz10). A-F, anterior dorsal, or posterior cervical, vertebra, element '2'; G-K, caudal vertebra, element '3'; and L, femur, element '7'; all from the 'small' individual, in: A, G, anterior; B, I, oblique antero-dorsal; C, oblique right antero-lateral; D, oblique right antero-lateral; E, ventral; F, J, posterior; H, L, dorsal; and K, left lateral views. Abbreviations: as for Text-figure 4.

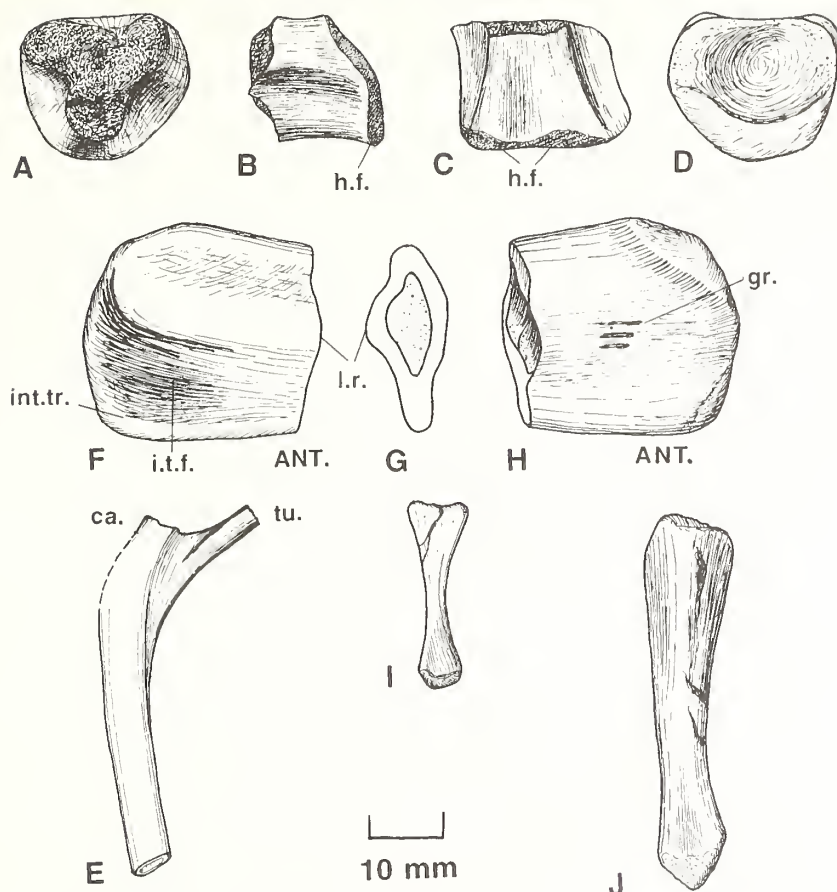
and its cross section changes from being a compressed oval at the proximal end to being more circular distally. The ventral surface of the bone is concealed by matrix, and cannot readily be prepared.

Other elements. Some other bones on the slab may pertain to the small prolacertiform. The thin curved sheet of bone ('17', Text-figs 2-3) located above elements '7' and '4' could be a fragmentary girdle element. Its overall shape and curvature suggest a partial coracoid, by comparison with *Macrocnemus* (Peyer 1937, figs 21-22; Rieppel 1989, figs 2-3). Beside it is an unnumbered thin strap-like element that widens towards one end, where a slight ridge also develops along the outer slightly curved margin. This could be a portion of cervical rib; it is located near the putative cervical vertebra '1'.

The large animal (Text-figs 2-3, 6)

Partial caudal vertebra. Partial vertebra '10' (Text-figs 2-3, 6A-D) is the posterior end of a centrum. The cross section is trefoil-shaped, the ventral margin of the centrum being rounded, and the sides expanding above a shallow groove on each side. Towards the posterior margin, the ventral surface expands, and is marked by a shallow midline groove behind two facets, presumably for a Y-shaped chevron (h.f., Text-fig. 6B-C). The posterior articular face of the centrum is subcircular in shape and slightly concave. If the vertebra were in proportion to the small caudal ('3', Text-figs 2-3, 5G-K), the preserved portion would represent only the posterior one-third or one-quarter of the centrum.

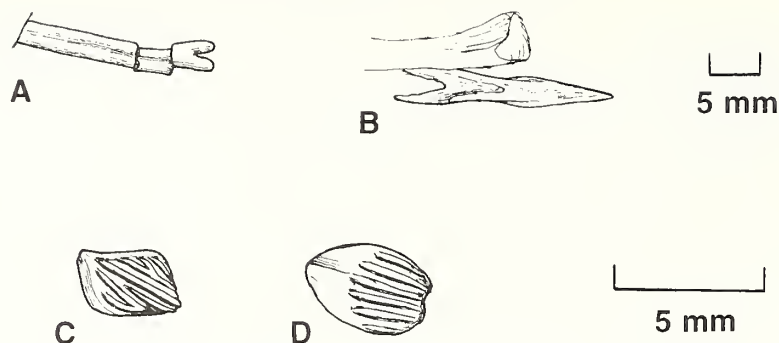
Rib. Element '9' (Text-figs 2-3, 6E) was not clearly identifiable until ADW prepared the specimen, and the proximal end was found to pass under element '5', and to branch. The shaft is nearly straight, and flattened



TEXT-FIG. 6. The type specimen of *Rhombopholis scutulata* (WARMS Gz10). A–D, partial caudal centrum, element '10'; E, rib, element '9'; F–H, proximal end of the right femur, element '4'; I, metacarpal, element '8'; and J, metatarsal, element '5', all of the 'large' individual, in: A, anterior; B, left lateral; C, F, I, ventral; D, posterior; G, cross sectional; and, H, J, dorsal views. Abbreviations: ANT, anterior; ca., capitulum; h.f., haemapophyseal facet; i.t.f., intertrochanteric fossa; int.tr., internal trochanter; l.r., lateral ridge; tu., tuberculum.

in cross section. The proximal head expands widely, and splits into capitulum and tuberculum (ca., tu., Text-fig. 6E). Both processes are broken and appear to be hollow, the capitulum being broad and bordering a depressed area that joins on to the smaller tuberculum, which is cylindrical in shape. The rib is presumably from the anterior thoracic region: it is too broad to be a typical cervical rib, and is double-headed. It is comparable to an anterior thoracic rib of *Macrocnemus* (Peyer 1937, p. 43, pl. 62, fig. 2a) or *Tanystropheus* (Wild 1973, fig. 35): mid- and posterior thoracic ribs are single-headed in these taxa.

Right femur. The proximal end of a large right femur ('4', Text-figs 2–3, 6F–H) was identified by Owen (1842a, p. 539) as possibly part of a large jaw bone, but further preparation of the back of the specimen by ADW has confirmed its true identity. The specimen is somewhat crushed. The proximal face is roughened, having possibly been cartilaginous and incompletely preserved. The lateral ridge (l.r., Text-fig. 6F–G) lies closer to the posterior margin of the element, and the bone surface passes into a slight convexity towards that margin. On the anterior side of the lateral ridge, the surface of the bone is more concave, and is rather deeply excavated towards the proximal margin, presumably forming the intertrochanteric fossa (i.t.f., Text-fig. 6F). This deep concavity becomes shallower and less pronounced distally.



TEXT-FIG. 7. The type specimen of *Rhombopholis scutulata* (WARMS Gz10). Postulated fish remains, probably palaeonisciform, possibly from *Gyrolepis*. A–B, isolated fish elements, possibly midline scales, elements 12 and 13; C–D, two scales, elements 11 and 16.

On the dorsal side of the bone (Text-fig. 6H), the surface is rather flat towards the anterior margin, but convex posteriorly. Near the proximal end are two broad roughened facets, the anterior of which may be an internal trochanter (int.tr., Text-fig. 6F). In the middle of the shaft are three or four deep longitudinal grooves (gr., Text-fig. 6H) that pass into the bone distally, possibly associated with the insertion of the puboischiofemoralis internus muscle.

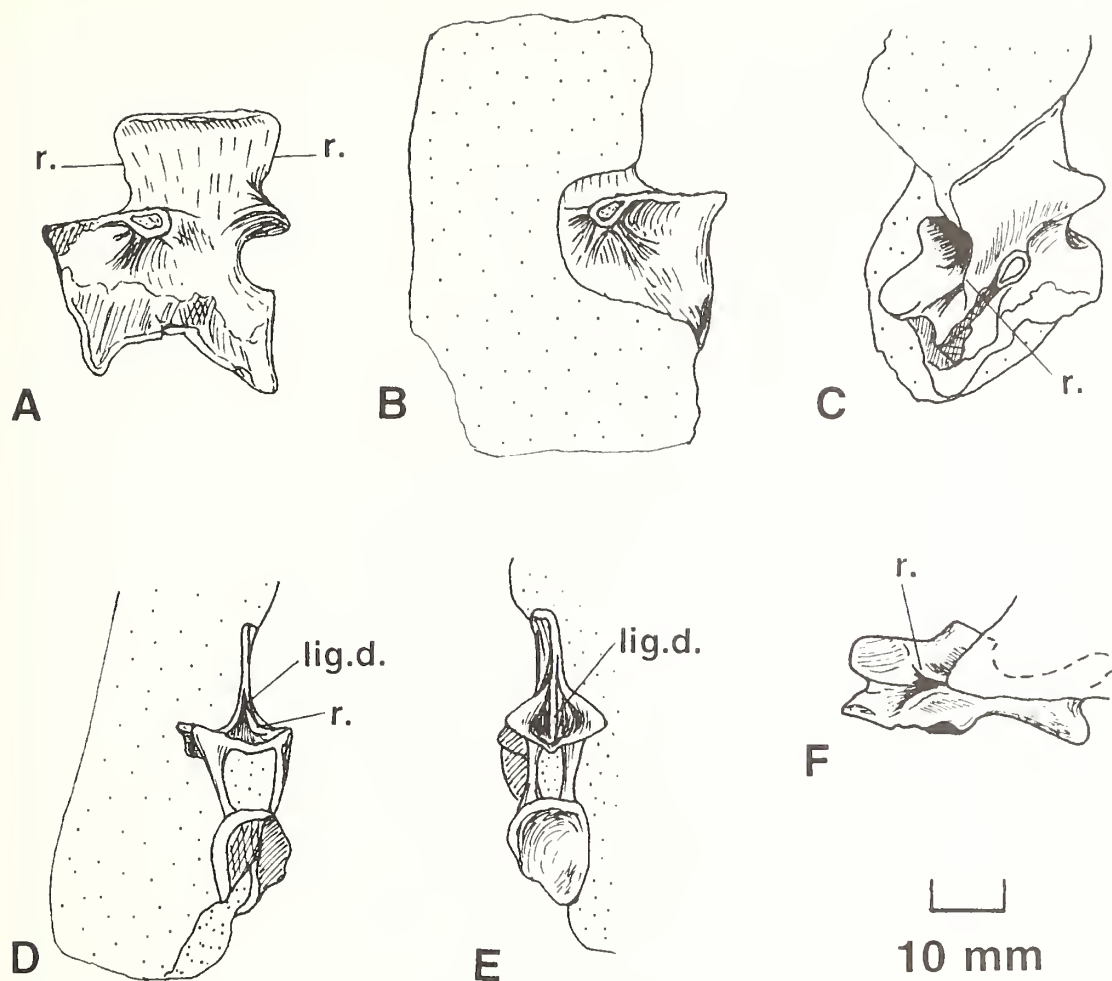
In overall shape, the proximal head of this femur is nearly indistinguishable from those of *Malerisaurus* (Chatterjee 1980, fig. 10, 1986, fig. 7), *Tanystropheus conspicuus* (von Huene 1932, fig. 3) and *T. longobardicus* (Wild 1973, fig. 73). The 'Cava Tre Fontane 1936' specimen of *Macrocnemus* (PIMUZ T2477) shows a near-identical slightly crushed right femur head, bearing also three or four grooves on the dorsal side, as in the present specimen (ADW, pers. obs.; pl. 1, fig. 2).

Metatarsal (?) A presumed metatarsal ('5', Text-figs 2–3, 6j), identified by Owen (1842a, p. 539) as a femur, matches the proximal femur end in size. This element cannot be a femur, or other major long bone, of the small animal since it is nearly symmetrical on the visible face. At the presumed proximal end, the element rises to a midline ridge on top, but is either flat, or slightly concave, below. The shaft in its middle portion is flat in cross section, and becomes only a little thicker towards the distal end. Distally, the shaft widens a little and a shallow midline concavity appears on the top surface. The articular facets at the distal end are rugose and unfinished, and the lateral angles may be missing. The whole element curves gently to the right, as viewed, and, if this edge is seen in dorsal view, this bone would be a left metatarsal. The proportions of the bone, and the markedly triangular proximal end, suggest that this is metatarsal IV, by comparison with the foot of *Macrocnemus* (Peyer 1937, pl. 55; Rieppel 1989).

Metacarpal (?) A postulated metacarpal ('8', Text-figs 2–3, 6i) is a smaller element. The exposed surface is relatively flat, and rather broader proximally than distally. The distal end is twisted 10–15° medially with respect to the rest of the bone. The distal articular facets are rugose and incomplete. If the element is viewed from its ventral surface, it is assumed to come from the left manus because the distal end twists slightly medially. In comparison with the manus of *Macrocnemus* (Peyer 1937, p. 66; Rieppel 1989, fig. 5), the proportions of length:maximum width, about 4:1, match metacarpals II or III best.

Palaeonisciform fish (Text-figs 2–3, 7)

The remaining elements may be fish bones ('12'–'15') and scales ('11', '16', and unnumbered). Element '12' (Text-figs 2–3, 8A) may be the 'fourth vertebra' referred to by Owen (1842a). It extends a long way beneath the rib '9', and its end could not be exposed during preparation by ADW; hence it cannot be a vertebra. It is a bilaterally symmetrical slender bone with a midline groove, and is rather damaged. It resembles, in its slenderness and mode of preservation, element '13' (Text-figs 2–3, 8B) which is also bilaterally symmetrical. Bone '13' appears to run to a point at one end, partly concealed by a scale below vertebra '3', and it bears a shallow groove along the midline, which deepens with a clear step about half-way along. The other end of bone '13', partly beneath the metacarpal '8', is divided into two narrow processes separated by a deep V-

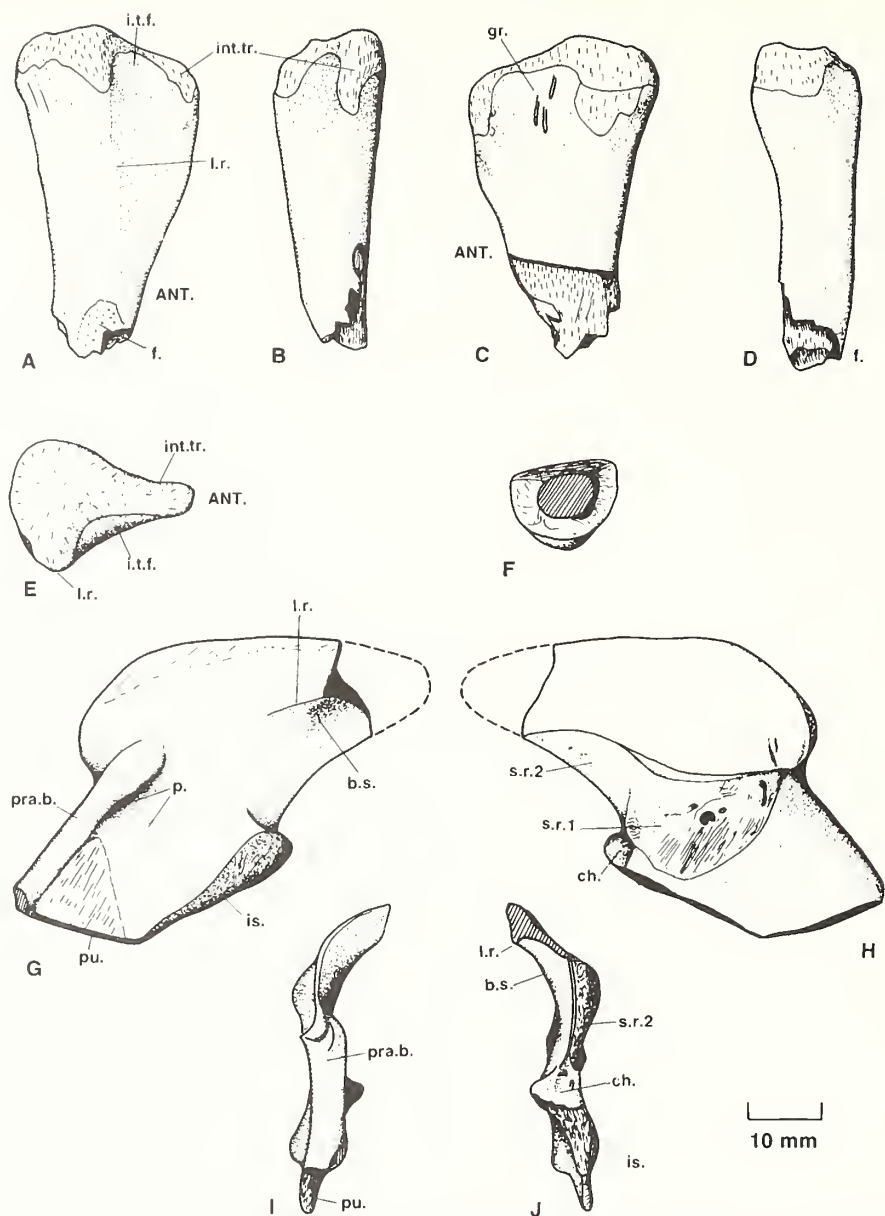


TEXT-FIG. 8. Dorsal vertebra of a prolacertiform, possibly *Rhombopholis* (CAMS M G.343), in: A, left lateral; B, right lateral; C, oblique left latero-dorsal; D, anterior; E, posterior; and F, dorsal views. The specimen is still partly enclosed in sandstone (broad stipple). Abbreviations: lig.d., insertion for ligamentum dorsale; r., ridge.

shaped notch. Elements '14' and '15' (Text-figs 2–3) may also be fish bones. The first is a straight flat element, slightly convex as viewed, and with a longitudinally striated surface. Element '15' is narrower, but also straight, and bearing a similar surface sculpture. It is broken, and its original size and shape cannot be determined. Owen (1842a, p. 539) referred to elements '13' and '14' as showing '...nearest resemblance to the ankylosed radius and ulna of the Frog'.

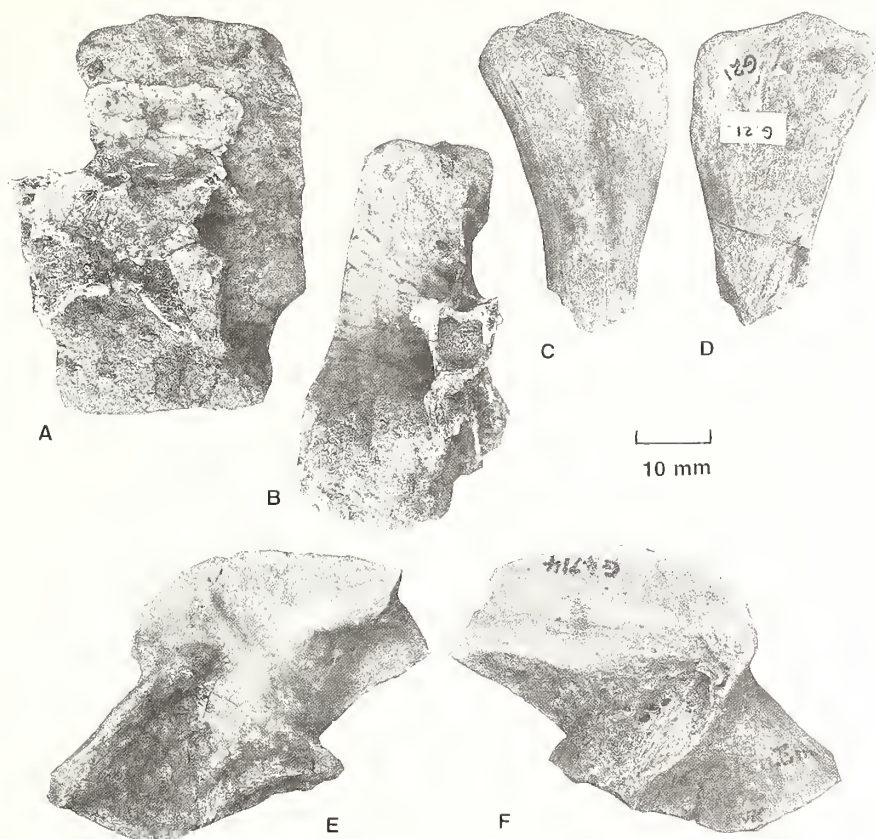
The fish scales, elements '11' and '16', as well as 13 other unnumbered examples (Text-figs 2–3) were identified by Owen (1842a, pp. 538, 540, pl. 46, fig. 5) as dermal scutes belonging, with the other bones, to the amphibian *Labyrinthodon*. The scale '11' (Text-fig. 7C) is rhomboid in shape, with rounded angles, and it bears a deeply incised sculpture of branching ridges, seven in all, running subparallel to the long axis, and extending into a slightly dentate posterior margin. The anterior margin is smooth, presumably where it was overlapped by adjoining scales. Scale '16' (Text-fig. 7D) is more ovoid, and the six longitudinal ridges do not branch. The anterior area of underlap is larger than in the preceding scale. In both cases, the ridged part of the scale is elevated above the level of the smooth area.

The identity of the fish bones and scales is difficult to determine. Element '13' (Text-fig. 7B) could be a midline fulcral scale from the dorsal or caudal fin, based on the observation of its symmetry, its thinness, and



TEXT-FIG. 9. Specimens of a prolacertiform, possibly *Rhombopholis*. A–F, proximal end of a left femur (WARMS Gz21), and G–J, left ilium (WARMS Gz4714), in: A, ventral; B, I, anterior; C, dorsal; D, J, posterior; E, proximal; F, distal; G, lateral; and, H, medial views. Abbreviations: ANT., anterior; b.s., brevis shelf; ch., channel; f., facet for muscle; gr., groove; i.t.f., intertrochanteric fossa; int.tr., internal trochanter; is., ischiadic facet; l.r., lateral ridge; p., pits; pu., pubic facet; pra.b., preacetabular buttress; s.r.1; s.r.2., attachment sites for sacral ribs 1 and 2.

the potential for the pointed end of an identical element to fit into the recessed V-shaped end. Element '12', also symmetrical and with a V-shaped end, could be some other midline scale. The other bones could be skull elements. The scales come from different parts of the body, the ovoid one ('16') possibly from the base of a fin or the tail.



TEXT-FIG. 10. Specimens of a prolacertiform, possibly *Rhombopholis*. A–B, dorsal vertebra (CAMSMS G.343), partly enclosed in sandstone, in: A, left lateral; B, anterior views. C–D, proximal end of a left femur (WARMS Gz21), in: C, ventral and D, dorsal views. E–F, left ilium (WARMS Gz4714), in: E, lateral and, F, medial views.

Comparison with common Middle Triassic fishes suggests that the bones and scales here may come from a paleonisciform bony fish such as *Gyrolepis*. The scales are very like those of typical *G. albertii* Agassiz, 1833, or some related species, common in the Muschelkalk of Germany (e.g. Oertle 1928, pp. 357–369, pls 31–32; Schmidt 1928, pp. 356–357). The genus *Gyrolepis* is known principally from the Middle Triassic of central Europe, but also from the Lower Triassic of eastern Asia, the Middle Triassic of South America, and the Upper Triassic of Europe and North America. The scales do not pertain to the perleidid *Dipteronotus* from the Bromsgrove Sandstone Formation and the Otter Sandstone Formation (Gardiner *in* Milner *et al.* 1990), the only other actinopterygian from rocks of this age in England. *Gyrolepis* has hitherto been recorded in England from the Upper Triassic Dane Hills Sandstone Member of Leicester (Horwood 1908; von Huene 1908*b*), from the Blue Anchor Formation (Tea Green Marl) of various localities (Warrington 1976), and from the Westbury Formation everywhere (Storrs 1994).

Other material of a 'large' prolacertiform (Text-figures 8–10)

Three other bones from the Bromsgrove Sandstone Formation may belong to the large prolacertiform, a dorsal vertebra (CAMSMS G.343), the proximal end of a left femur (WARMS Gz21), and possibly a left ilium (WARMS Gz4714).

Dorsal vertebra. Vertebra CAMSMS G.343 (Text-figs 8, 10A–B) is slightly crushed, and lacks the left surface of the centrum. It has been prepared to show the left side and part of the right-hand side. The centrum is deeply

constricted ventrally and laterally, and its articular ends are set at a slope of about 20° from the vertical. The anterior articular face of the centrum is broken away, and the posterior face is largely filled with sediment, but it is deeply concave, and ovoid in shape. There is no parapophysis.

There is no evident suture between the centrum and neural arch. The neural canal is nearly square in anterior view, and is narrower in posterior view. The prezygapophyses bear broad circular articular facets, oriented outwards at an angle of 10° or less above horizontal. Two ridges (r., Text-fig. 8C–D, F) run from the anterior margin of the neural spine to the prezygapophyses. The prezygapophyseal shelf extends back to form the anterior margin of the transverse process, which is directed a little upwards. Neither transverse process is complete, but the right-hand one (Text-figs 8B–D, F, 10B) shows most detail. The process is a thin lamina anteriorly that thickens backwards above three radiating narrow buttresses (Text-fig. 8B), strikingly similar to those in a mid-dorsal vertebra of *Tanystropheus* (Wild 1973, fig. 54).

The postzygapophyses (Text-figs 8A, C, E–F, 10A) bear broad subcircular articular facets oriented at a low angle above horizontal. The postzygapophyseal pedestals run high up the posterior margin of the neural spine. The neural spine is a tall subquadratic thin sheet of bone with a near-vertical anterior margin (Text-figs 8A, 10A), which splits into two sharp ridges, on either side of a deep cleft for the ligamentum dorsale (lig.d., Text-fig. 8D). The top of the neural spine is nearly at right angles to the anterior margin, and there is only a slight expansion. There appears to be a narrow midline lamina of bone on the posterior margin of the spine, presumably the site of insertion of the ligamentum dorsale (lig.d., Text-fig. 8E).

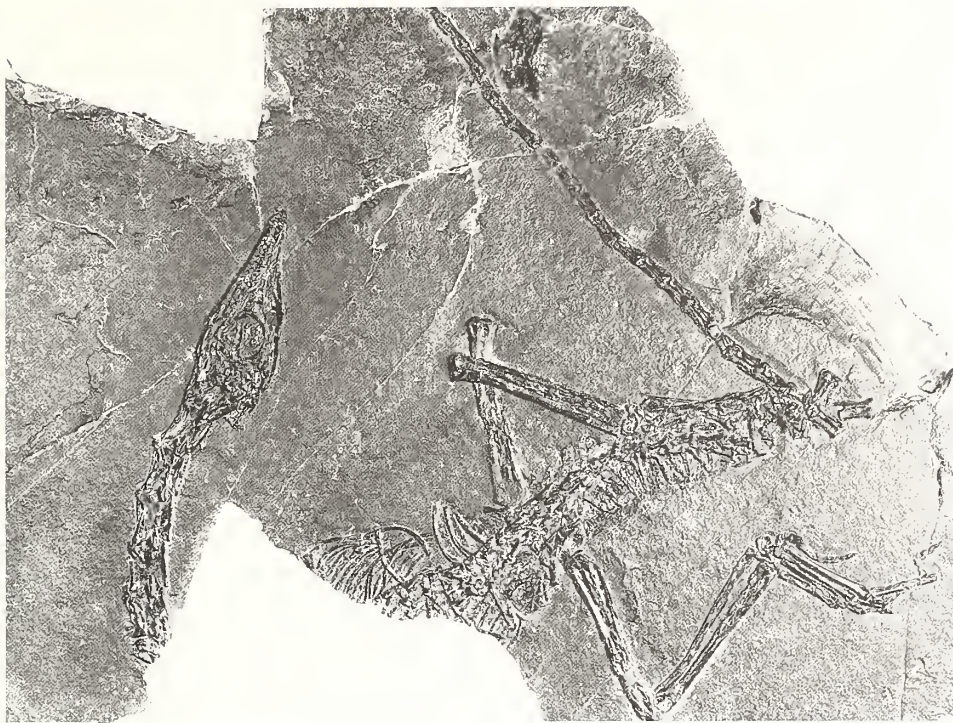
This vertebra is presumably a middle to posterior dorsal, since it lacks a parapophysis (present in cervicals and anterior dorsals of *Macrocnemus* and *Tanystropheus*; Peyer 1937; Wild 1973). The overall shape, with a high neural spine, indicates a vertebra from the lumbar region, by comparison with *Macrocnemus* and *Tanystropheus* (Wild 1973, fig. 54). The vertebra shows two characters noted by Peyer (1937, p. 19) as typical of *Macrocnemus*: the neural spines are long and adjacent ones would touch when the vertebrae are articulated. The latter feature is seen also in *Prolacerta* (Colbert 1987, p. 11) and *Malerisaurus* (Chatterjee 1980, p. 17), but these taxa seem to have rather shorter neural spines, although Gow (1975) noted that neural spine length alternates between short and long in the dorsal vertebral column of *Prolacerta*. The 'Cava Tre Fontane 1936' specimen of *Macrocnemus* (PIMUZ T2477) shows a longitudinal ridge or lamella between the prezygapophysis and the transverse process in three mid-dorsal vertebrae, although their transverse processes seem to be wider (ADW, pers. obs.; Pl. 1, fig. 2).

Left femur. The proximal end of a left femur (WARMS Gz21) is similar in size to the large proximal femur end '4' in WARMS Gz10, but rather more of the specimen is preserved, extending to the shaft. The specimen is virtually uncrushed, but is rather eroded. The expanded proximal end bears a substantial lateral ridge (l.r., Text-fig. 9A, E), running close to the posterior side. The heavily abraded proximal articular surface consists of a major ovoid head on the posterior side and a lower narrower anterior expansion terminating in the internal trochanter (int.tr., Text-fig. 9A–B, E). There is a deep intertrochanteric fossa (i.t.f., Text-fig. 9A, E) near the proximal end. Near the distal margin, the ventral ridge dips into the beginning of a rugose flat facet, possibly part of a muscle insertion site (f., Text-fig. 9A, D).

The dorsal face of the bone (Text-figs 9C, 10D) is rather flatter than the ventral, showing a slight convexity distal to the main articular head, and a slight concavity anteriorly. There are also three or four sharp-sided grooves deepening into the bone distally in this area (gr., Text-fig. 9C), as in WARMS Gz10 (cf. Text-fig. 6H). These grooves lie in a slightly concave area, presumably representing the insertion point of the puboischiofemoralis internus muscle. The shaft is slender and subtriangular in section distally (Text-fig. 9F), and contains a subcircular sediment-filled cavity.

EXPLANATION OF PLATE 1

Figs 1–3. Specimens of *Macrocnemus bassanii* (von Nopcsa, 1931). 1, the 'Alla Cascina, 1933' specimen (PIMUZ A III/208), showing a good head and neck, a partial posterior trunk, hindlimbs, and tail; $\times 0.7$. 2, the 'Cava Tre Fontane, 1936' specimen (PIMUZ T2477), showing a skull, partial hindlimb and pelvic girdle, and anterior tail; the right femur lies at top left just beside the back of the skull; the left ilium lies just left of the snout tip, and the left femur and lower limb just below; the anterior caudals are seen in ventral view in the bottom left-hand; $\times 0.85$. 3, the 'Point 902, 1960' specimen (PIMUZ T2470), a detail showing the left ilium and ischium in contact, viewed medially (ilium to the right) and the left femur viewed laterally; $\times 0.5$.



1



2



3

The original lengths of the two large proximal femoral fragments, in WARMS Gz10 and Gz21, may be estimated by comparison with *Macrocnemus*. In the least crushed example, 'Besano II' (PIMUZ T2476), the femur is 72 mm long and 15 mm wide, a ratio of proximal breadth:length of 4.8. Scaling with this factor, the large femur in WARMS Gz10 would have been approximately 144 mm long, and femur WARMS Gz21 would have been 134 mm long.

Left ilium. The left ilium (WARMS Gz4714) is nearly complete, missing only the tip of its posterior dorsal process, and being abraded a little at the anterior end of the iliac blade, and along the pubic and ischiadic facets (Text-figs 9G–H, 10E–F). The dorsal blade has a short anterior process and a longer posterior one. The dorsal margin is thin, curves gently posterolaterally when viewed from above, and the blade is nearly vertical in its anterodorsal portion. There is a slightly roughened area along the anterior portion of the dorsal edge of the iliac blade, probably for the origin of the iliotibialis muscle. A marked ridge rises on the lateral face (l.r., Text-fig. 9G) and extends towards the missing posterior tip. The ridge is roughly triangular in section, and marks the upper margin of a deeply excavated recess, the brevis shelf (b.s., Text-fig. 9G, J), the probable site of origin of the iliofibularis and caudifemoralis brevis muscles. At this point, the iliac blade bends sharply down to a narrow ventral margin. A channel runs from below the lateral ridge, round the posterior margin of the iliac neck, and below the sacral rib attachments where the surface is rugose (ch., Text-fig. 9H, J).

The acetabular region of the ilium is broad (Text-figs 9G, 10E). The anterior edge is greatly thickened as a strong column of bone, a preacetabular buttress, that starts high on the blade as a rounded projection (pra.b., Text-fig. 9G, I). Behind this, the acetabulum is shallow and bears two deep pits (original or damage?) at the top (p., Text-fig. 9G), and a roughened area below which may mark an area of cartilage. The posterior margin of the acetabulum is also thickened. The ventral articular surfaces for the pubis and ischium are clearly set off (pu., is., Text-fig. 9G): the latter is more massive. The preacetabular buttress and the posteroventral region of the acetabulum bear a rugose ornament.

In medial view (Text-figs 9H, 10F), the ilium is divided into three areas. The dorsal part of the blade is smooth, and curves up and laterally to the thin dorsal edge. Beneath this is a rugose and pitted triangular area, bearing two facets, a large subcircular one for the distal end of sacral rib 1, and a smaller triangular one for sacral rib 2 (s.r.1, s.r.2, Text-fig. 9H). The latter facet is set at a sharp angle to the former. Below these facets, a convex surface forms the medial wall of the acetabulum, and curves round to join the preacetabular buttress.

Relatively few prolacertiform ilia have been illustrated with sufficient clarity for comparisons to be made. The ilium of *Prolacerta* (Gow 1975, fig. 24A) seems strikingly similar, having a heavy preacetabular buttress, a long posterior iliac blade, a short anterior process, and a marked lateral ridge. *Malerisaurus* also has a marked lateral ridge, and the outline shape of the ilium (Chatterjee 1980, fig. 10a) is similar to WARMS Gz4714, as is that of *Tanystropheus* (Wild 1973, fig. 71). The 'Point 902 1960' specimen of *Macrocnemus* (PIMUZ T2470) shows an excellent left ilium (Pl. 1, fig. 3) which is like WARMS Gz4714, although it is about half the size (ADW, pers. obs.).

COMPARISONS

The specimens described here could belong to a variety of animals. There are five sets of materials to be assessed, assuming that the specimens assigned to the 'small individual' and the 'large individual' on WARMS Gz10 have been correctly associated. These five sets are the two groupings on WARMS Gz10, the dorsal vertebra (CAMSM G.343), the left ilium (WARMS Gz4714), and the partial left femur (WARMS Gz21). The tetrapods that may be considered include temnospondyl amphibians, procolophonids, rhynchosaurs, trilophosaurs, prolacertiforms, archosaurs, and synapsids, all typical of Middle Triassic terrestrial faunas (e.g. Benton 1983a; Benton *et al.* 1994).

Temnospondyls and procolophonids may be ruled out, since all elements – vertebrae, limb girdle bones, and limb bones – are quite different in appearance. Likewise, the vertebrae and limb elements cannot be matched with any Triassic synapsid taxon (cf. Kemp 1982). As for archosaurs, most Middle Triassic groups (e.g. Erythrosuchidae, Ctenosauriscidae, Proterochampsidae, Rauisuchidae, Poposauridae) were much larger than these elements, and none of the bones corresponds (cf. Charig *et al.* 1976). The dorsal vertebra (CAMSM G.343) could be interpreted as archosaurian, but the neural spine and centrum are much longer anteroposteriorly than in corresponding dorsals of a variety of Triassic archosaurs (Charig *et al.* 1976, pp. 49, 50, 104). The ilium and the femora cannot

be matched with any known archosaur, and indeed there is no sign of a fourth trochanter, an archosaur synapomorphy, in the present material. The groups remaining for consideration are the rhynchosaurs, trilophosaurs, and prolacertiforms.

None of the bones can be compared to those of rhynchosaurs, whether small or large ones (von Huene 1938; Benton 1983*b*, 1990). Rhynchosaurs have short neural spines on their cervical and dorsal vertebrae, and the cervicals are not elongate. The ilium of *Rhombopholis* is most like that of the much larger *Stenaulorhynchus* (von Huene 1938), but the rhynchosaurs have a more symmetrical iliac blade, with no sign of the sharp lateral ridge, and a much weaker preacetabular buttress. The femoral head is similar, but it is narrower and the articular head projects further proximally in rhynchosaurs than in *Rhombopholis*.

Some of the present material could be classed as trilophosaurid. The vertebrae, however, do not correspond (cf. Gregory 1945, pls 23–25), the cervicals being shorter and higher, and the dorsals having much taller neural spines in *Trilophosaurus*, and differing considerably in detail (ADW, pers. obs. of BMNH R8302). The caudal vertebra (Gregory 1945, pl. 24) is comparable in shape, but in features common to many reptile groups. Further, only mid-tail caudals of *Trilophosaurus* are comparable to that of *Rhombopholis*, but the former have very short transverse processes (ADW, pers. obs. of BMNH R8302). The ilium of *Trilophosaurus* (Gregory 1945, pl. 28) shares a very short anterior iliac blade with *Rhombopholis*, but lacks a marked lateral ridge and preacetabular buttress. Further, the posterior process of the iliac blade seems much longer in *Trilophosaurus* than in WARMS Gz4714. The femoral head in *Trilophosaurus* (Gregory 1945, pl. 29) is massive and more equidimensional in cross section than in *Rhombopholis*. This was confirmed by direct comparison with a left femur of *Trilophosaurus* (ADW, pers. obs. of BMNH R8302). Further, the internal trochanter is not set off as such a distinctive narrow flange in *Trilophosaurus*. On balance, a case could be made that the isolated ilium and femoral head (WARMS Gz4714, Gz21) are trilophosaurid, and the vertebrae probably are not. However, the association of the proximal femur head in WARMS Gz10 with clearly non-trilophosaurid vertebrae suggests that these postcranial elements are not trilophosaurid either. The femur WARMS Gz21 is like the larger one in WARMS Gz10, although the ilium cannot be directly linked with the 'large animal' in WARMS Gz10.

The only group remaining are the prolacertiforms, a clade ranging from Late Permian (*Protorosaurus*) to Late Triassic (*Tanystropheus*). The low long cervical vertebra, the square-spined dorsals, the strong preacetabular buttress on the ilium, and the broad-headed slender femur are all shared between *Rhombopholis* and *Protorosaurus*, *Prolacerta*, *Macrocnemus*, *Malerisaurus*, and *Tanystropheus*, and the first three of these at least appear to be synapomorphies of the Prolacertiformes, or of included clades within that group. The closest resemblances of the *Rhombopholis* specimen, and the other material described here, seem to be with *Macrocnemus bassanii* (Pl. 1). In an unpublished cladistic analysis of prolacertiforms recently completed by MJB and J. A. Allen (Bristol), only five of 48 characters could be recorded for *Rhombopholis*. This was insufficient to distinguish *Rhombopholis* from other prolacertiform taxa, such as *Prolacerta*, *Macrocnemus* and *Malerisaurus*, and hence its position in the cladogram could not be determined meaningfully.

It is assumed that the reptilian bones described here represent two individuals of similar taxa, one of which is three to four times smaller than the other. None of the bones may be compared directly between the small and large animal, but both appear to be prolacertiforms. The smaller one could be a juvenile of the larger, although it lacks clear osseous indicators of juvenility: for example, the neural spines are fused to the vertebral centra, where in true juveniles a suture might still be visible.

Rhombopholis is different in size from known specimens of *Macrocnemus*. For example, femur lengths in *Macrocnemus* range from 45 to 93 mm (Peyer 1937; ADW, pers. obs.), compared with about 50 mm (preserved length of element '7' in WARMS Gz10, 44 mm) for the small English individual, and 140–150 mm for the large individual. The latter is, however, exceeded in size by species of *Tanystropheus*, with femur lengths of 48–212 mm in *T. longobardicus* (Wild 1973), and 305 mm in *T. conspicuus* (Wild 1973), and *Tanytrachelos* with femur lengths of 173–303 mm (Olsen

1979), but is similar to *Malerisaurus*, which has femur lengths of 100–120 mm (Chatterjee 1980, 1986).

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ULTRASTRUCTURE OF *SYNORISPORITES DOWNTONENSIS* AND *RETUSOTRILETES* CF. *CORONADUS* IN SPORE MASSES FROM THE PRÍDOLÍ OF THE WELSH BORDERLAND

by D. EDWARDS, K. L. DAVIES, J. B. RICHARDSON, C. H. WELLMAN and L. AXE

ABSTRACT. Scanning and transmission electron microscopy has been employed to describe the ultrastructure of constituents of two kinds of spore masses recovered on bulk maceration of basal Downtonian (Prídolí, Silurian) sedimentary rocks from the Welsh Borderland. Spores of *Synorisporites downtonensis*, occurring as tetrads in narrow, elongate masses, possess a thick homogeneous exospore. Adjacent tetrads are linked by sporopollenin bridges. Variation in distal sculpture is discussed in relation to spore ontogeny. Discoidal masses contain *Retusotriletes* cf. *coronadus* also isolated from coeval *Pertonella dactylethra*, the sporangia of which are of similar shape to those of *Cooksonia pertoni* and also terminate smooth isotomously branching axes. However, differences in ultrastructure of exospore, that in *R. cf. coronadus* shows faint striations, with a darker layer bordering the lumen, compared with the bilayered exine of *Cooksonia* spores, suggest that the two megafossil species are not closely related.

RECENT studies describing spores from a number of late Silurian and earliest Devonian plants have begun to demonstrate the potential of spore features as useful taxonomic characters in plants of simple morphology, when preserved as small coalified fragments (Fanning, Richardson and Edwards 1991; Edwards *et al.* 1994). In the case of *Cooksonia pertoni* Lang, 1937, sporangia have been shown to contain one of four taxa of dispersed spores that are similar in their equatorially crassitate structure and bilayered exospore, but differ in their distal sculpture (Fanning *et al.* 1988; Rogerson *et al.* 1993; Edwards *et al.* 1995). Here we extend our ultrastructural studies to *Synorisporites downtonensis* Richardson and Lister, 1969, the genus being recorded (as *S. verrucatus*) in *C. pertoni* subsp. *synorispora*, and to *Retusotriletes* cf. *coronadus*. The latter occurs in *Pertonella dactylethra* Fanning, Edwards and Richardson, 1991, a rhyniophytoid with sporangia identical in shape to those of *C. pertoni*, but bearing prominent spines (Fanning, Edwards and Richardson 1991).

LOCALITY DATA

1. Ludford Corner

Platyschisma Shale Member, Downton Castle Sandstone Formation, Prídolí Series. Eight elongate spore masses comprising *Synorisporites downtonensis* were picked out following bulk maceration of a siltstone layer 1.6 m above the top of the main bone bed at this famous locality in the small cliff at the junction of Ludford Lane (Whitcliffe Road) and Leominster Road (A49), c. 75 m south-south-west of Ludford Bridge, Ludlow [SO 5122 7412] (White and Lawson 1989). The exact location of a further three is less secure, but probably is at the same level or just below it.

2. Weir Quarry

Platyschisma Shale Member, Downton Castle Sandstone Formation, Prídolí Series. A single specimen with *Synorisporites downtonensis* was isolated from a siltstone clast c. 35 mm above a bone

bed (possibly equivalent to the main Ludlow Bone Bed) from an overgrown quarry *c.* 275 m north-east of Bringewood Forge Bridge, Downton Castle Estate, near Ludlow [SO 4560 7525] (Richardson and Rasul 1990).

3. *Perton Lane*

Rushall Beds (equivalent in the Woolhope Inlier of the Downton Castle Sandstone Formation), Přídolí Series. Two spore masses with *Retusotritetes* cf. *coronatus* were isolated from a buff, fine-grained micaceous sandstone just above a bone bed thought to be equivalent to the Ludlow Bone Bed at Ludford Lane. The horizon is in a small cutting on the eastern side of the lane leading to Perton Quarry, Stoke Edith, and to Copgrove near Hereford [SO 5971 4035] (Squirrell and Tucker 1960).

Spore assemblages from the horizons yielding spore masses at all three localities belong to the *Synorisporites tripapillatus* – *Apiculiretusispora spicula* Assemblage Zone (Richardson and McGregor 1986) which encompasses the base of the Downtonian and is considered equivalent to the lower part of the Přídolí Series.

TECHNIQUES

Conventional procedures for preparation of palynological samples were employed, except that centrifugation was omitted. Spore masses were picked out under a dissecting microscope, mounted on stubs, air dried and coated for SEM (Cambridge 360). One specimen from each locality was then prepared for TEM (Rogerson *et al.* 1993; Edwards *et al.* 1995). It was first divided into three, and a part mounted for light microscopy (LM). Prior to embedding and sectioning, one of the remaining fragments was treated with fuming nitric acid. Qualitative X-ray (energy-dispersive) microanalysis capable of detecting elements above sodium (atomic number 11) was employed on semi-thin sections of spores with blue-green interference colours using a Philips 300TEM. All stubs, grids and slides are housed at the National Museum and Gallery of Wales. Additional SEM images collected via a PC-based image capture and storage system are stored on hard disc (WORM drive). Selected images will be transferred to CD-ROM (durable non-fading format not subject to accidental erasure) to be deposited with the specimens.

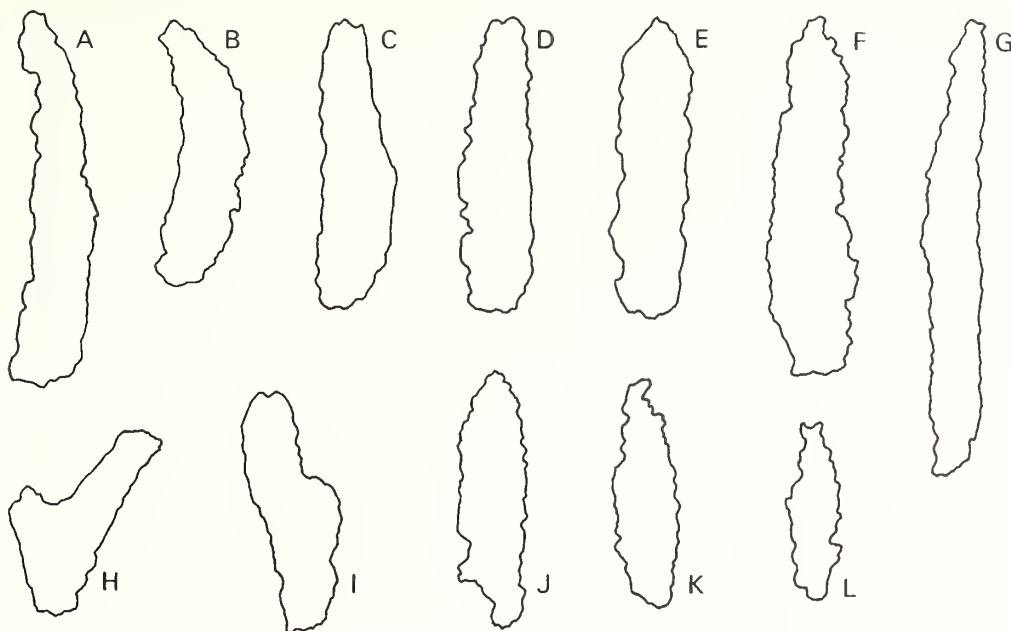
Terminology. This follows earlier usage (Rogerson *et al.* 1993) where the presumably sporopollenin-impregnated, acetolysis-resistant spore wall is called the exospore ($\equiv$ exine).

SPORE MASSES WITH *SYNORISPORITES DOWNTONENSIS*

Description

SEM observations. Very narrow elongate spore-masses recovered from Ludford Lane (11) and Weir Quarry (one) are unusual in that the spores occur in tetrads (Text-fig. 1; Pls 1–3). Such masses range from 543 to 1490 μm long and 158 to 289 μm maximum width. They were probably circular in cross section with a maximum of 6 tetrads/diameter. Plate 1, figure 4 shows a typical representative with a tapering, probably complete rounded end while the other is irregular, truncated and probably fractured. The lateral contours are slightly and irregularly undulating except where tetrads are missing (Pl. 1, figs 3, 5). One example is bifurcated (Pl. 1, fig. 6). In a few cases, irregular fragments of a sheet-like material adhere to peripheral tetrads (Pl. 1, figs 7–8). This is interpreted as the remnants of a sporangial wall. It is usually a single, somewhat shredded layer with no indications of organization, with the possible exception of the fragment illustrated in Plate 3, figure 5 (arrowed).

The exposed distal surfaces of the spores are ornamented by muri (Pl. 1; Pl. 2, figs 1–9) except near the equator which is usually smooth. The width and prominence of this equatorial border varies between spore masses as do the shape, dimensions and resulting relief of the ornament. In many



TEXT-FIG. 1. Outline of elongate spore masses containing *Synorisporites downtonensis*. All from Ludford Lane, except G which is from Weir Quarry. A, NMW95.19G.1; B, NMW95.19G.5; C, NMW95.19G.2; D, NMW95.19G.12; E, NMW95.19G.13; F, NMW95.19G.3; G, NMW95.19G.7; H, NMW95.19G.6; I, NMW95.19G.9; J, NMW95.19G.4; K, NMW93.143G.8; L, NMW95.19G.8. All $\times 40$.

examples with well-defined ornament, the tetrads are connected by 'bridges' extending between usually distal peripheral muri (Pl. 3, figs 9–10). No such junctions occur in the tetrads of one specimen where the ornament is least developed and marked by sinuous grooves (Pl. 2, fig. 3) such that the surface appears flattened to slightly undulating. Gentle prodding with a needle usually separated the tetrads into individual components and revealed conspicuous triradiate folds, with interradiate irregular muri on the proximal surface giving a puckered effect (Pl. 2, figs 10–12; Pl. 3, figs 1–3). Muri may be absent near the proximal pole (Pl. 3, fig. 3) in some spores. Fortuitous separation of a tetrad shows continuity between the irregular proximal muri of adjacent monads (Pl. 3, fig. 7) although in others the proximal faces are completely separate (Pl. 2, fig. 11), the tetrad forming a hollow sphere of almost lenticular spores. An equatorial thickening cannot be distinguished in SEM, but this region appears to form a rigid marginal equatorial feature, sometimes accentuated by some inward collapse of the proximal surface but usually more sharply delimited on the distal. Further evidence for this comes from the more or less circular cracks on distal surfaces in one specimen (Pl. 2, fig. 3) where it is postulated that final stages in sporopollenin deposition have not been completed (see later). Such cracks are typically produced by radial stress during shrinkage with fracture occurring along weaker areas, in this case close to the inner limits of the marginal band. In all specimens the trilete mark is represented by a triradiate narrow fold, straight or slightly sinuous (Pl. 3, figs 1–3), extending to the equatorial feature.

Dimensions of sporangial masses and spores are given in Table 1. In some masses, the tetrads appear almost uniform in size and spherical in shape (Pl. 1, fig. 2), and are usually loosely packed. Where more variable in size, this is not gradational along the mass. Differences in appearance result from depressions in tetrads (either at the junction between three spores (Pl. 2, fig. 8) or on distal surfaces (Pl. 2, fig. 7)), degree of separation and sometimes slight overlap of the tetrad components (Pl. 2, fig. 9). Variation in distal ornament may relate to developmental stage (see later).

TEM observations. Sections are similar with and without fuming nitric acid treatment in both samples, with the 'best' sections from the Ludford Lane material. Their most distinctive features are the thick homogeneous exospore, electron-dense bodies in the lumen and the complete absence of any extra-exosporeal material. The exospore is conspicuously thicker in distal rather than proximal walls, with spore orientation determined by size and nature of ornament in section (Pl. 4, figs 1–4). There is little variation in total thickness of the distal wall, but in some sections, the proximal wall shows increase in width at the periphery of the spore (Pl. 4, fig. 3). Otherwise there is no pronounced equatorial thickening. Structurally the exospore appears uniform except at its inner and outer limits. Differences in intensity and extent of staining (minus acid treatment) in the outermost exospore in four spores from Ludford Lane shown in Plate 4, figures 2–9, 11–13 furnish inconclusive evidence for a very narrow (*c.* 1.2 μm wide) outer layer. Well-defined superficial layering is also present in some Weir Quarry spores. In one of two examples showing reversed staining (Pl. 4, fig. 10) this might reflect increased physical resilience (probably due to greater reinforcement by resin), because the rest of the spore has puckered/shattered on sectioning.

The innermost layer is of variable thickness, may be separated from the rest of the exospore by small voids (Pl. 4, figs 11–13) or may show further layers to the inside (Pl. 4, fig. 11). In the latter example, this might reflect the remains of spore contents sandwiched between proximal and distal wall inner layers, especially as the darkly staining elliptical bodies may also be so enclosed (Pl. 4, figs 11–12). Plate 4, figure 13 shows an example where these bodies of variable shape and size occur in a lighter homogeneous matrix filling the lumen of the cell. In a similar example from Weir Quarry, the darker bodies are surrounded by voids and more disorganized material which stains similarly to or less densely than the exospore. In other cases the lumen is marked by a space lined by the dark bodies. The nature of the innermost wall layer, be it part of the exospore, endospore or remains of spore contents, remains conjectural. The darkly staining bodies were originally thought to be pyrite, but this is unlikely as they survive nitric acid treatment. Traces of iron and sulphur along with silica and chlorine (from resin) were recorded in X-ray microanalysis, with highest peaks identified as tin (from the grid) copper (specimen holder) and calcium (?indigenous).

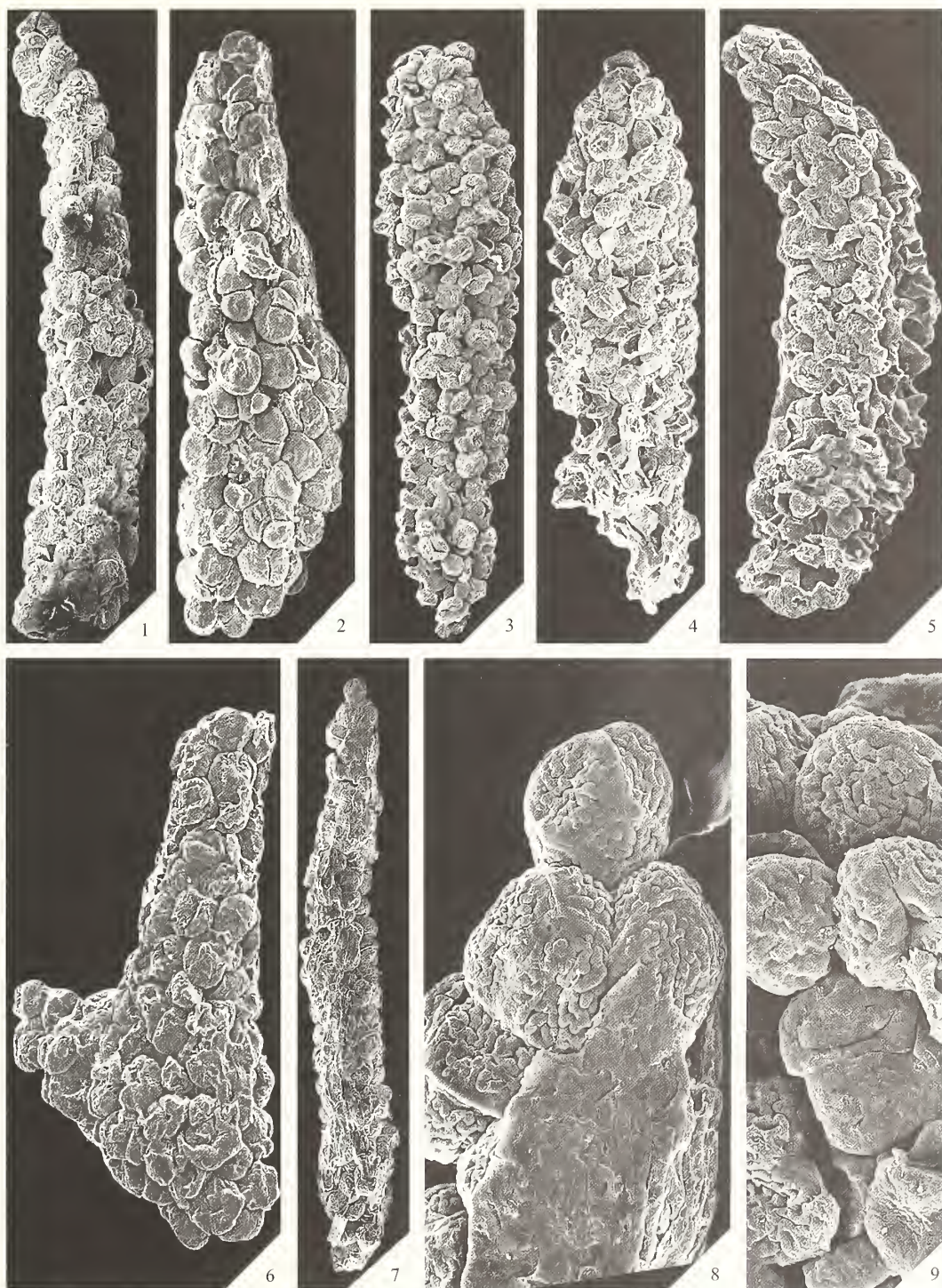
Distal ornament produces an undulating surface contour with more or less smooth curves (Pl. 4, figs 2–3), both higher and wider in cross section than the proximal, where the outline is more angular and less regular, sometimes almost serrated (Pl. 4, figs 3–4). Connections (bridges) between ornament in adjacent proximal faces in the same tetrad (Pl. 4, fig. 3) and distal faces of adjacent tetrads (Pl. 4, fig. 4) show no variation in ultrastructure, nor junctions. The illustrated section through a triradiate mark is tangential and probably close to the equator (Pl. 4, fig. 1). The apertural fold in SEM is seen in this LM section as a triangular projection but with little change in appearance or thickness of exospore because the lumen projects a short distance into the base of the structure.

Identification of spores and plant affinity

The distinguishing generic features of these spores necessitating assignment to the genus *Synorisporites* are the prominent curvaturae perfectae forming a more or less rigid equatorial

EXPLANATION OF PLATE 1

Figs 1–9. SEMs of spore masses of *Synorisporites downtonensis* Richardson and Lister; Přídolí Series, Welsh Borderland (distal ends to top of plate). 1, NMW95.19G.1; Ludford Corner; $\times 80$. 2, NMW95.19G.2; Ludford Corner; $\times 98$. 3, NMW95.19G.3; Ludford Corner; $\times 80$. 4, NMW95.19G.4; spore mass with incomplete development at presumed proximal end; Ludford Corner; $\times 108$. 5, NMW95.19G.5; anomalous development at base and on left hand side; Ludford Corner; $\times 108$. 6, NMW95.19G.6; bifurcating spore mass; Ludford Corner; $\times 123$. 7, NMW95.19G.7; slender elongate mass with adhering non-cellular material; Weir Quarry; $\times 60$. 8, magnification of one end of 7; $\times 380$. 9, variation in distal ornament in single spore mass illustrated in fig. 3; $\times 450$.



EDWARDS *et al.*, spore masses of *Synorisporites*

crassitude, which is cuneiform in section, and the murornate distal sculpture. Other genera with similar structure are *Ambitisporites* (laevigate), *Streelispora* and *Aneurospora* (apiculate). The spores illustrated here in SEM and TEM are identical to the dispersed spore species *Synorisporites downtonensis*. The nature of the murornate sculpture, particularly on the proximal surface, and the relatively large size of the spores distinguishes this species from all described contemporary *Synorisporites* species. The proximal sculpture was originally described by Richardson and Lister (1969) as having contact areas covered with irregular convolute muri somewhat angular in plan, rounded to conical in profile. It thus differs from the smaller *S. tripapillatus* in the absence of interradian papillae, while *S. verrucatus* lacks proximal muri and possesses verrucate-murate distal ornament. Richardson and Lister isolated *S. downtonensis* from dispersed spore assemblages from Ludford Lane and Downton Gorge (Weir Quarry) but always as monads. However, they recovered similar spores, the best preserved as tetrads, from Lower Ludlow rocks. They called these cf. *S. downtonensis* because they had insufficient information on proximal characters for secure identity. In the light of our study it seems likely that the older spores are conspecific, but were then released into air currents as tetrads rather than monads.

Scanning electron microscopy indicates pronounced differences in both proximal and distal ornament from *Synorisporites verrucatus*, which occurs usually as monads in *Cooksonia pertoni* subsp. *synorispora*, and is also dispersed in discoidal masses. They also differ ultrastructurally, with *S. verrucatus* possessing a bi-layered exospore, the outer layer comprising c. < 20 per cent. of the total wall diameter. *In situ* spores of *S. verrucatus* occur in an inter-spore matrix which includes a peripheral layer around each spore and they lack any evidence of junctions between spores. Thus although the spores described here and those in *Cooksonia pertoni* subsp. *synorispora* are placed in the same spore genus, they derive from plants differing in a number of sporangial characters, including shape. Such plants were probably of differing affinity, and certainly not members of the *Cooksonia* lineage (Edwards *et al.* 1995).

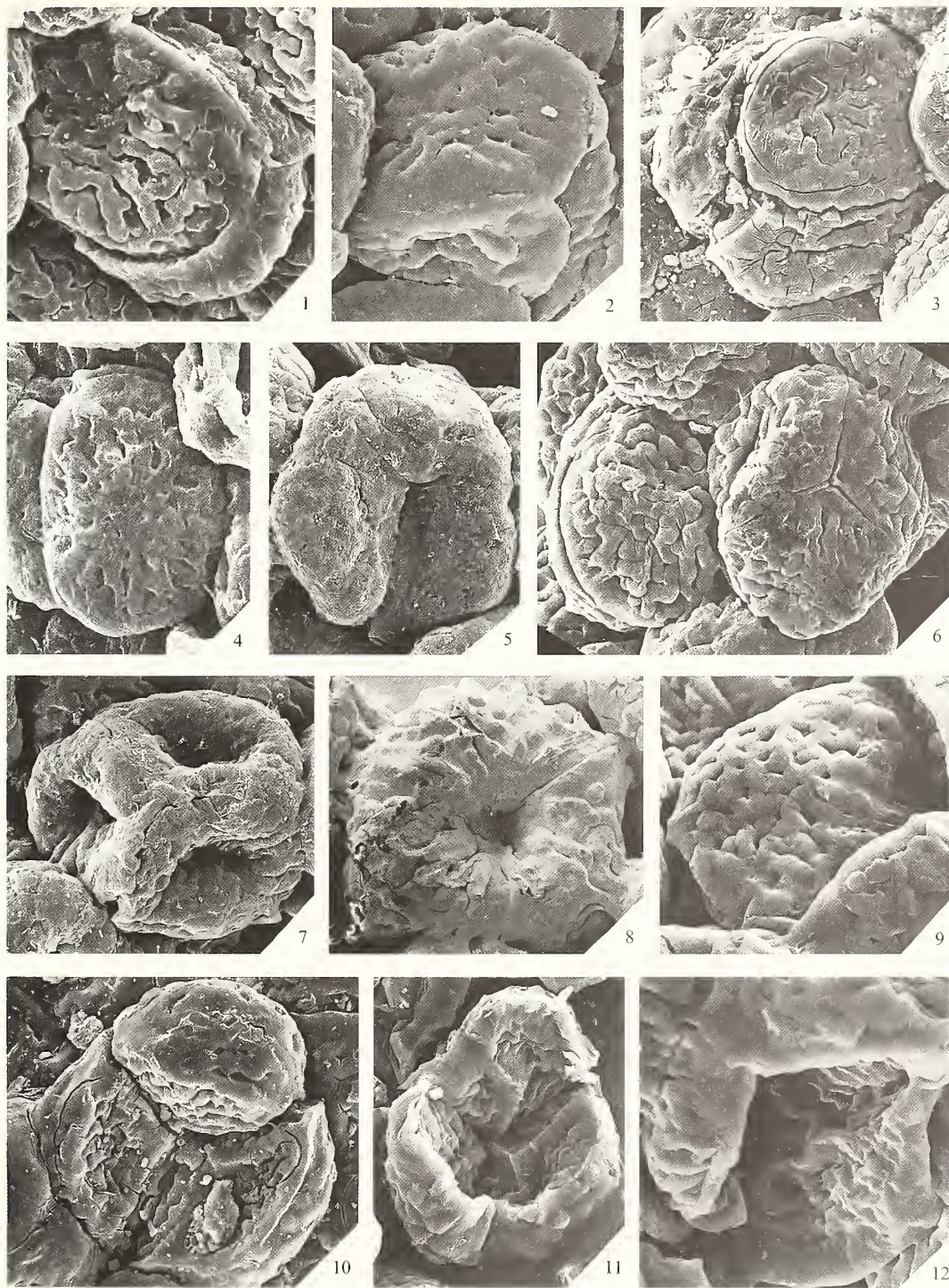
The combination of tetrads, elongate shape, lack of perispore or any indications of tapetal activity in the form of globules preclude relationship with any Upper Silurian and Lower Devonian plant fossils with *in situ* spores yet described (e.g. Fanning *et al.* 1988; Edwards 1996; Edwards and Richardson in press).

Considering broad affinity with higher groups based on extant homosporous plants, the presumed lack of perispore eliminates ferns *sensu lato*, sphenopsids, some homosporous lycopods (Tryon and Lugardon 1991) and mosses, although there is, of course, the possibility that ancient members of a group had different characters from their descendants. The shape of the spore mass is not like that of any fossil or extant Lycopodiales. This leaves the liverworts for more detailed consideration, particularly in relation to trilete marks, persistent tetrads and sporangial shape. Triletes characterize Marchantiales and Anthocerotales, but are not present in taxa such as *Haplomitrium* (Jungerman-

EXPLANATION OF PLATE 2

Figs 1–9. SEMs of *Synorisporites downtonensis* Richardson and Lister, illustrating variation in distal surfaces and equatorial features of spores in tetrads. Fig. 1, Weir Quarry; figs 2–9, Ludford Corner; both Pridoli Series, Welsh Borderland. 1, NMW95.19G.7; $\times 700$. 2, NMW95.19G.6; $\times 825$. 3, NMW95.19G.2; radial stress fractures. These are unlikely to have been produced by beam damage as they are absent from all the other specimens similarly processed; $\times 520$. 4, from the same mass as fig. 2; $\times 700$. 5, NMW95.19G.3; $\times 650$. 6, NMW95.19G.8; $\times 550$. 7, NMW95.19G.3; inward collapse at distal pole; $\times 700$. 8, NMW95.19G.1; collapse at contact between three spores; $\times 600$. 9, NMW95.19G.4; $\times 1000$.

Figs 10–12. SEMs of *S. downtonensis* spores in which one member of the tetrad has become displaced revealing the proximal surfaces of the remaining three. All from Ludford Corner, Pridoli Series, Welsh Borderland. 10, from the same mass as fig. 3; $\times 575$. 11, from the same mass as figs 5 and 7; $\times 625$. 12, from the same mass as fig. 9; $\times 1000$.



niales) where spores adhere in loose tetrads, or in *Sphaerocarpos* (Sphaerocarpaceae) where they do not usually separate. In species that do, there is no trilete mark (Doyle 1975). In some tetrads, components appear to be held together by bridges (e.g. *Sphaerocarpos donnellii*; see Long 1993, fig. 5). Occasional wide bridges between distal surfaces of adjacent spores have been figured in the jungermannialean, *Chandonanthus squarrosus* (Taylor *et al.* 1974). On the basis of shape, the elongate masses of *S. downtonensis* might have derived from an anthocerotalean type of sporangium, but there is no evidence of a columella. Although this structure is absent at maturity in sporangia of certain species of *Anthoceros*, it seems unlikely it was ever present in the masses described here because of the homogeneity of the masses. Thus, by a process of elimination and some disparate similarities, the spore-masses might well have derived from hepatic-like plants where sporangial wall and vegetative tissues lacked the recalcitrant polymers enhancing fossilization potential. In this respect the absence of sporopollenin-impregnated elaters is not critical as they are not universal in liverworts.

Observations on spore development

The significance of the relatively undifferentiated structure of the exospore in terms of affinity is conjectural. While it might well represent the true nature of the exospore at spore maturity, it is also possible that diagenesis has obliterated any substructure, although layering has been observed in different contemporaneous taxa at this and other localities. In most of the spore masses, there is very little variation in spore size and distal ornament throughout the specimen, with persistent connections between tetrads throughout. This seems to indicate synchronous maturation within the sporangium (if sporangial contents are indeed preserved in their entirety). The development of the sporopollenin bridges between ornament on adjacent tetrads is suggestive of polymerization of a final coating of sporopollenin as locular fluid was withdrawn, perhaps accompanied by shrinkage and separation of the tetrads. Whether or not such bridges were mere by-products of development or had the function of holding spores together in the living plant, perhaps ensuring dispersal in clumps, cannot be ascertained. Their absence on tetrads where ornament is marked by sinuous grooves on an otherwise more or less smooth surface, suggests that the distal ornament was formed by a final phase of sporopollenin deposition on a template possibly initiated by the sporocyte or more probably the spore. In the specimen lacking pronounced ornament (Pl. 2, fig. 3), proximal surfaces of the spores are still in contact although not linked. The circular fractures mentioned earlier and small 'crazed' fractures not seen on other specimens suggest different properties of the wall prior to fossilization. That these tetrads are larger than the others might be seen as evidence against an immaturity hypothesis. It is however possible that the spores shrank during the final phase of sporopollenin development, and as they did so produced the bridges. The gametophytic control element of the hypothesis appears to find some support in three specimens where atypical

EXPLANATION OF PLATE 3

Figs 1–12. SEMs of *Synorisporites downtonensis* Richardson and Lister; Ludford Corner, Pridoli Series, Welsh Borderland. 1–3, proximal surfaces. 1, NMW95.19G.9; $\times 825$. 2, NMW95.19G.4; $\times 1075$. 3, NMW95.19G.3; note flattened areas in interradian region at pole; $\times 875$. 4–6, regions of spore masses showing incomplete development of tetrads which are often linked by broad bands of sporopollenin. 4, NMW95.19G.5; $\times 270$. 5, NMW95.19G.5; possible wall fragment is arrowed; $\times 320$. 6, NMW95.19G.3; $\times 380$. 7, NMW95.19G.1; bridges between proximal faces of members of same tetrad; $\times 1100$. 8, NMW95.19G.3; indistinct bridges (top left) between adjacent tetrads where distal ornament is poorly developed; $\times 825$. 9, NMW95.19G.8; prominent bridges between adjacent tetrads with well-defined ornament; $\times 590$. 10, as for 9, NMW95.19G.4; $\times 1200$. 11, NMW95.19G.4; pyrite damage on incompletely developed spore; $\times 2100$. 12, NMW95.19G.4; broad bridge between spores with incompletely developed ornament; $\times 675$.

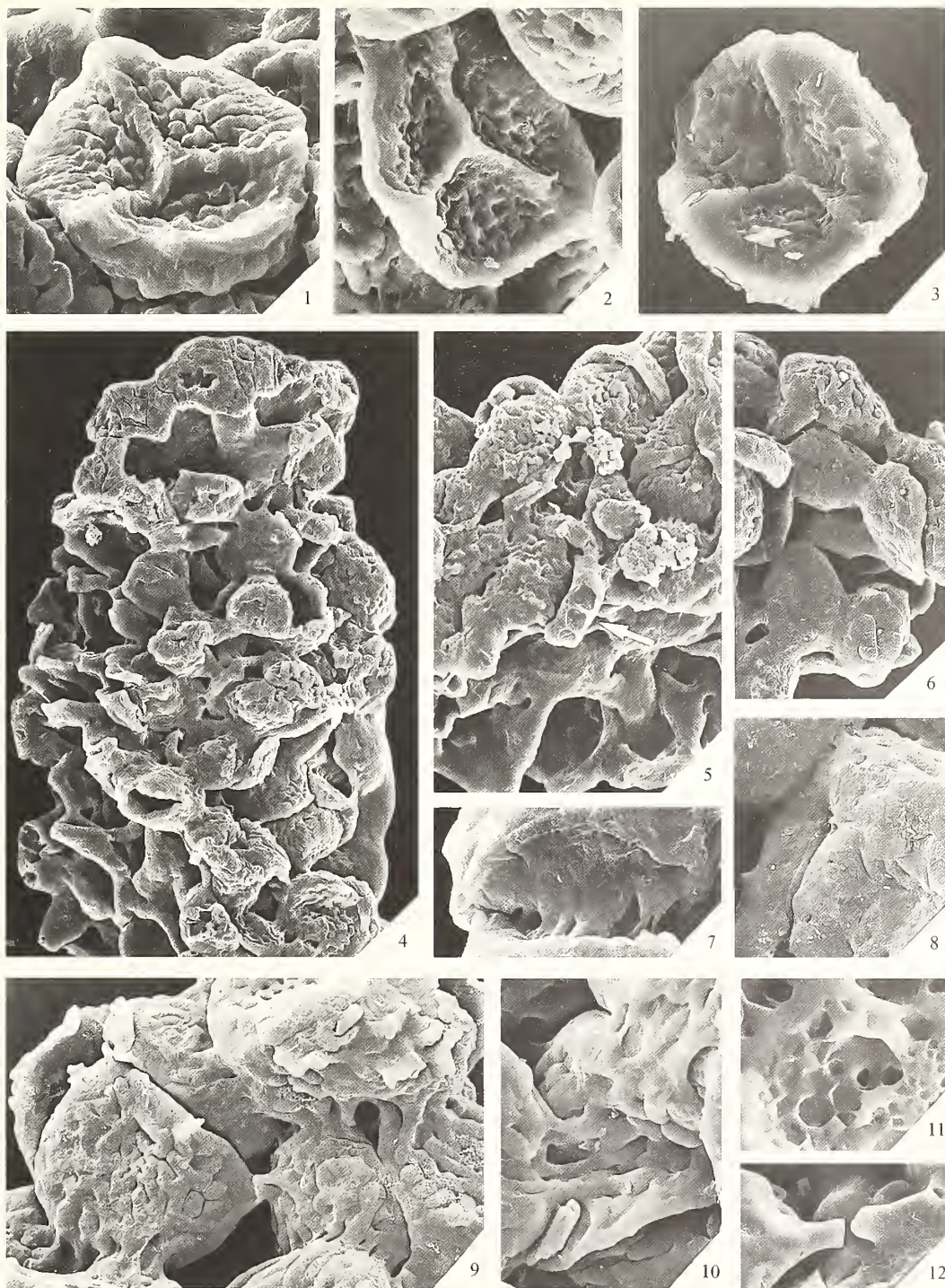
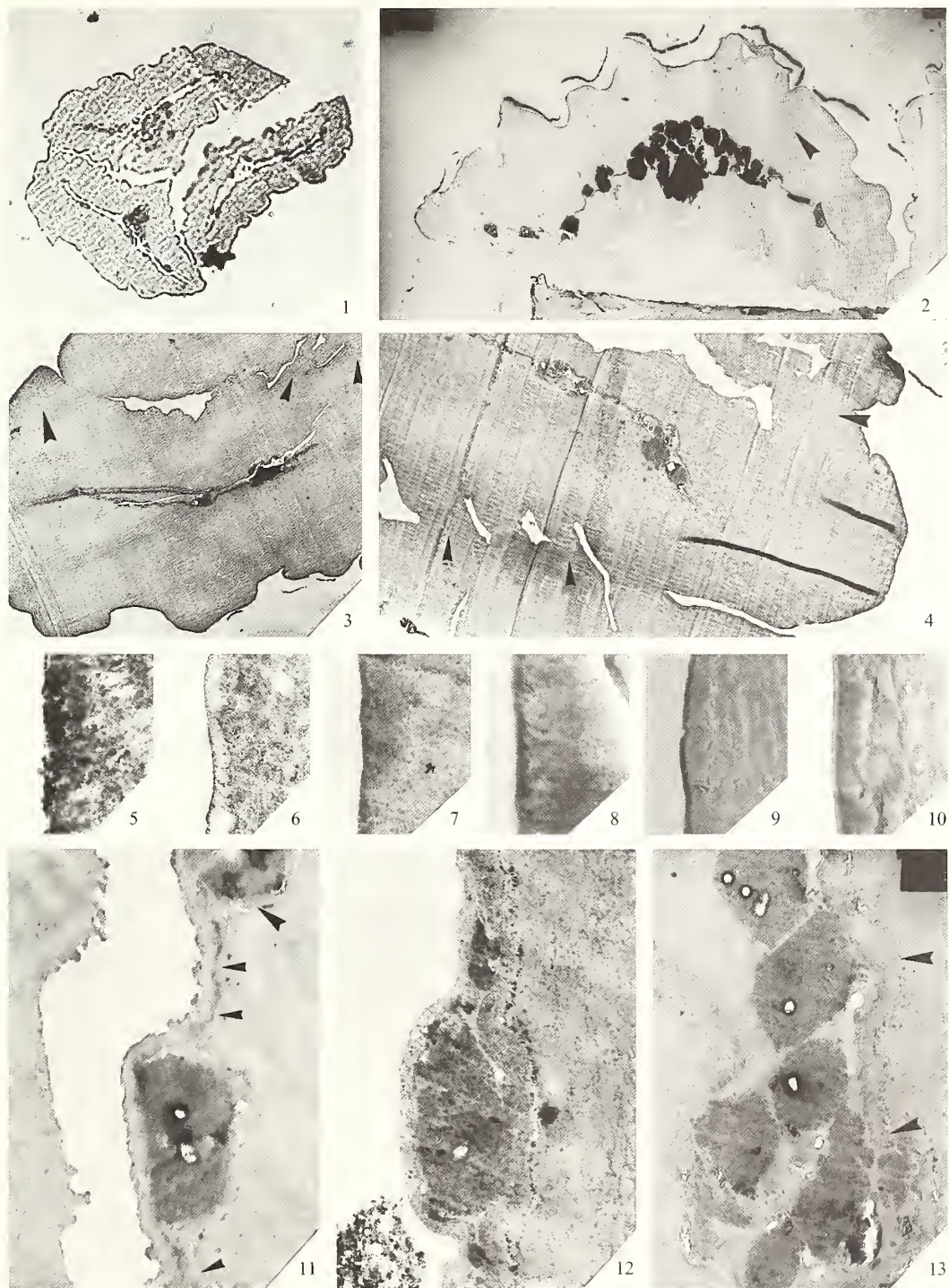


TABLE 1. Data for spore masses comprising *Synorisporites downtonensis*. All from Ludford Lane except NMW95.19G.7 (Weir Quarry)

Specimen number	Length of spore mass (μm)	Width of spore mass (μm)	+ / - Forked	Monad dimensions (μm)	Tetrad dimensions (μm)	c. No. of tetrads in spore mass
NMW95.19G.3	1170	289	—	40 (48) 55, $N = 13$	58 (66) 76, $N = 20$	375
NMW93.143G.8	915	215	—	44 (53) 59, $N = 13$	62 (71) 80, $N = 20$	181
NMW95.19G.1	1180	220	—	48 (54) 63, $N = 11$	65 (78) 86, $N = 20$	132
NMW95.19G.9	850	220	—	49 (55) 60, $N = 13$	66 (74) 81, $N = 11$	113
NMW95.19G.5	790	250	—	50 (53) 55, $N = 7$	64 (72) 87, $N = 12$	147
NMW95.19G.6	580	158	+	50 (55) 59, $N = 12$	56 (68) 78, $N = 16$	62
NMW95.19G.8	543	183	—	55 (58) 60, $N = 10$	63 (74) 83, $N = 16$	50
NMW95.19G.4	825	226	—	40 (43) 49, $N = 19$	51 (59) 68, $N = 20$	228
NMW95.19G.7	1490	207	—	53 (58) 62, $N = 11$	62 (72) 83, $N = 12$	192
NMW95.19G.2	957	260	—	52 (59) 65, $N = 8$	75 (85) 93, $N = 6$	117
NMW95.19G.12	960	240	—	54 (59) 62, $N = 4$	63 (77) 82, $N = 15$	134
NMW95.19G.13	945	220	—	54 (59) 63, $N = 3$	67 (72) 82, $N = 10$	89

EXPLANATION OF PLATE 4

Figs 1–13. *Synorisporites downtonensis*; figs 1 and 10 Weir Quarry (NMW95.19G.7); remainder Ludford Corner (NMW93.143G.8); both Přídolí Series, Welsh Borderland; all nitric acid treated. 1, LM of section through three of four members of a tetrad. Note ridges marking arms of trilete, $\times 610$. 2–13, TEMs. 2, section through complete spore with thicker distal wall (arrow). Electron-dense bodies occupy lumen. Detached dark line represents gold coating. Note differences in contours of distal and proximal surfaces; $\times 1435$. 3, walls of two adjacent spores with junction between proximal faces (small arrows). Note increase in thickening at margin of proximal wall (large arrow) in spore where distal wall also present; $\times 2470$. 4, bridges (arrows) between distal surfaces of adjacent spores, and at margin of proximal face (large arrow); $\times 3260$. 5–10, variation in appearance of outermost part of distal wall. 5, $\times 15000$. 6, $\times 12500$, 7, $\times 20200$. 8, $\times 20000$. 9, $\times 10000$. 10, $\times 15000$. 11–13, sections through lumen region following nitric acid treatment. 11, large lighter area is space resulting from the breakage of a discontinuous layer marked by arrows on the intact side; $\times 18000$. 12, as for 11 with additional darkly staining granules at the line of weakness; $\times 17300$. 13, larger densely staining bodies in light amorphous matrix, bordered by slightly darker layer separated from rest of exospore by a row of small irregular voids (arrows: large arrow in 11); $\times 11000$.



tetrads are present. Typical tetrads occur at the attenuated (?intact) apex, but collapsed, fragmentary or poorly defined tetrads occur elsewhere. In some cases these spores show weakly defined distal ornament (Pl. 2, figs 2, 5, 7) and may have collapsed centripetally producing a hollow spherical structure (Pl. 2, fig. 11). In other examples, ornament or, in some cases, even the rounded outline of a spore cannot be detected and the tetrads are replaced by interconnecting straps or sheets (Pl. 3, figs 4–6). The latter sometimes bear the imprint of pyrite crystals (Pl. 3, fig. 11) perhaps indicating that the sporopollenin impregnated wall was softer when the mass was fossilized. The one specimen (Pl. 1, fig. 4) where such spores are concentrated at one end might provide evidence for continued meiosis and spore production at the base of a sporangium, as occurs in extant *Anthoceros*. However, in the two other cases the region of abnormal tetrads extends along one side of the mass and is probably more indicative of meiotic failure. This suggests that all the sporangial contents, whether ?sporocytes, aborted spores or fully developed tetrads, were coated in the final phase of sporopollenin deposition. If the verrucate patterning had been determined by the sporophyte, as in extant liverworts (Brown *et al.* 1986), it would be expected to have been present on the incompletely developed spores, as has been shown in extant angiosperms where 'normal' patterning occurs on aborted pollen (e.g. Tischler 1908). However, based on his very detailed studies on exine and exospore development, J. R. Rowley (Stockholm) considers it very unlikely that 'changes in exine form continue following the death of the microspore' (pers. comm. 1995; Rowley and Flynn 1969). The abnormal spores and fragments described here, with their unornamented walls, support such an interpretation of gametophytic control.

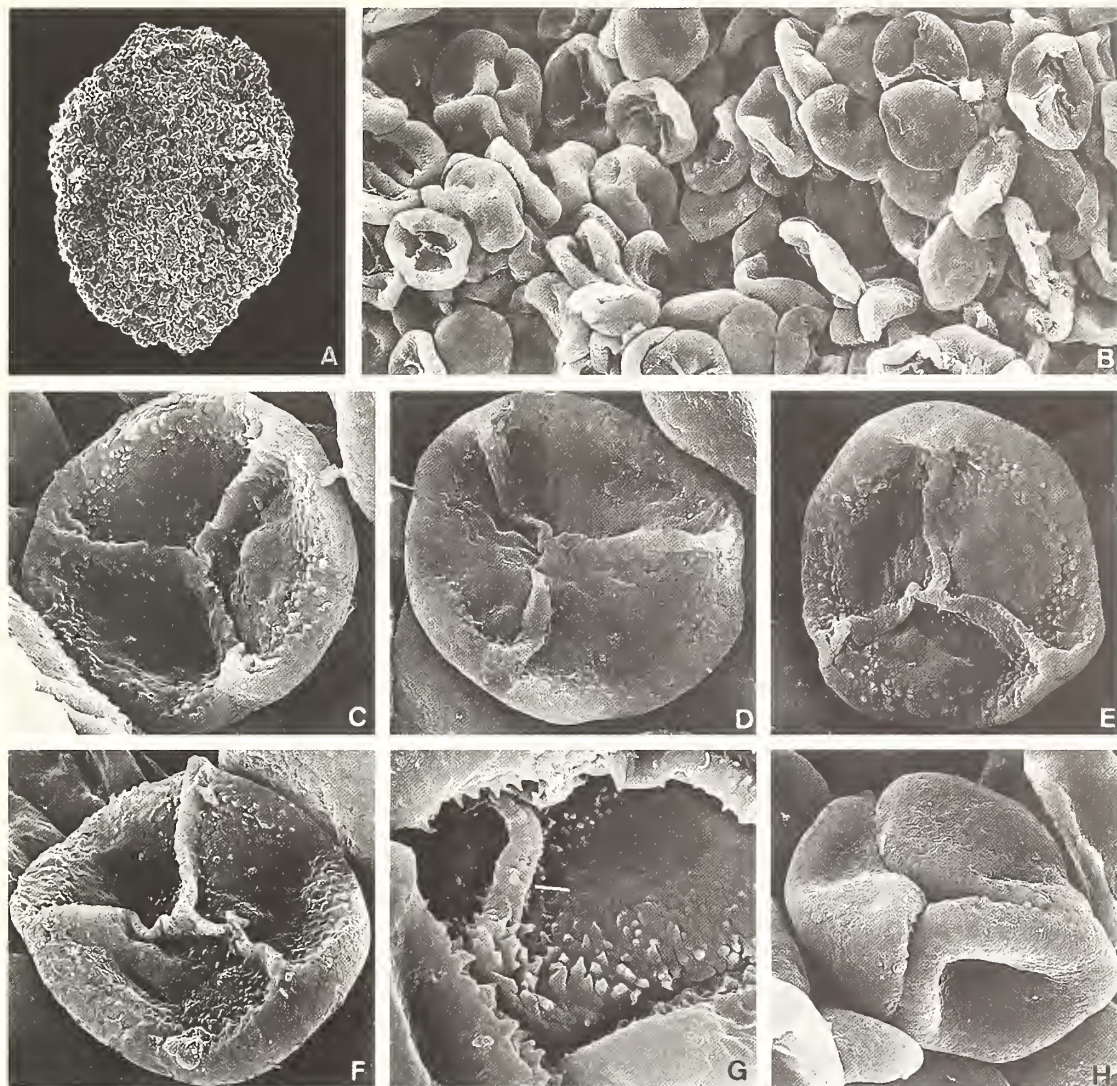
SPORE MASSES WITH *RETUSOTRILETES* CF. *CORONADUS*

Description

SEM observations. Spores of similar morphology to those in the two masses described here, but of greater diameter, were recorded in sporangia of *Pertonella dactylethra* from Perton Lane. One of the spore masses (Text-fig. 2A) from the same locality is discoidal and of such dimensions (0.94 mm × 0.68 mm) that it probably represents the entire contents of a single sporangium of *P. dactylethra*. The other is less regular in shape, and spores have more pronounced proximal ornament. Neither has any indications of the sporangial wall, nor of any extrasporal material. Dimensions of sporangial masses and spores are given in Table 2.

The spores have a circular to subcircular amb (Text-fig. 2B). The exospore is rigid, but often invaginated over the proximal surface (Text-fig. 2E). Trilete folds are prominent, sinuous, almost reach the equator and often bear grana and microconi scattered on the folds and forming bands (1–4 µm wide) on the flanking proximal exospore on both sides of the trilete folds (Text-fig. 2C–F). At or near the radial apices the trilete folds and their sculptural bands coalesce with a sculptured zone forming proximal and subequatorial *curvaturae perfectae*; bands (3–4 µm wide) comprise minute sculptural elements; *curvatural* and proximal sculptural elements, ± isodiametric (< 1 µm), consist of grana, microconi and microbaculae (Text-fig. 2G). Distal (Text-fig. 2H), equatorial and proximal triangular areas (between *curvaturae* and trilete sculptural bands) are laevigate.

TEM observations. Sections taken from the discoidal spore mass are noteworthy in showing a minimum of sectioning artefacts. Unlike in *Synorisporites downtonensis* there are major differences in appearance after nitric acid treatment which obliterates the layering typical of untreated specimens as seen in Plate 5, figure 1. In this almost complete section, the distal wall is of more or less uniform width, thicker than the proximal and laevigate on the surface, while the proximal is thinnest in the region of the apertural fold (c. 30 per cent. of the width of the opposing distal wall) and increases in thickness towards the equator. This variation in thickness results in a caving inwards of the central area of the proximal wall, a phenomenon also noted in the SEMs (Text-fig.



TEXT-FIG. 2. SEMs of spore mass (A; NMW95.19G.10) and its contained spores (B–H), which are assigned to *Retusotriletes* cf. *coronatus*, Perton Lane, near Hereford, Welsh Borderland; Přídolí Series. All, except E, untreated with nitric acid. A, $\times 46$; B, $\times 610$; C–F proximal surface. C, $\times 2050$; D, $\times 1900$; E, $\times 1950$; F, $\times 1900$; G, ornament on proximal surface, trilete fold arrowed, $\times 3900$; H, three members of a tetrad, $\times 1375$.

TABLE 2. Data for spore masses comprising *Retusotriletes* cf. *coronatus* from Perton Lane, Přídolí Series.

Specimen number	Length of spore mass	Width of spore mass	Spore dimensions (μm)
NMW95.19G.11	860 μm	680 μm	20 (24) 30, $N = 18$
NMW95.19G.10	940 μm	680 μm	20 (22.5) 27, $N = 20$

2C–F). Both proximal wall and apertural fold bear occasional, irregularly sized and distributed cones (Text-fig. 2C–G). At low magnifications, the lumen appears bounded by a dark line and contains intensely staining, discrete rounded or oval bodies or rounded to oval bodies. At higher magnification, in some sections, the boundary layer is further resolved into a dark line and inner layer with irregular inner limit (Pl. 5, fig. 4) immediately adjacent to the lumen. In others the darker layer fades into the rest of the exospore, but internally is continuous with very disorganized, almost fibrillar, material within the lumen where it may also partially encase the very electron-dense bodies (Pl. 5, fig. 5). The rest of the spore wall may appear homogeneous (Pl. 5, fig. 4) or show traces of very faint striations (Pl. 5, fig. 5).

The darker layer around the lumen enters the base of the apertural fold (Pl. 5, figs 1–2) and extends into it as diffuse lines (Pl. 5, fig. 3), indicating that the wall of the fold is of similar width to the immediately adjacent proximal wall.

None of this layering is visible after nitric acid treatment (Pl. 5, figs 2, 7), and a reticulum in the lumen marks the original position of the darkly staining bodies (Pl. 5, figs 1–2). In some areas there is a faint indication of spongy texture in the innermost part of the wall itself (Pl. 5, fig. 7).

We have no information on the nature or composition of the dark bodies: the fibrillar material surrounding them might represent the remains of cell contents, although its continuity with the exospore is puzzling. The darker lines which disappear on acid treatment might represent the coalified residues of cellulose, perhaps part of the endospore. Equally conjectural are the origins of the faint striations parallel to the exospore surface, in that they could represent a compressed multifoliate structure, possibly even the vestiges of the lamellae seen in certain fossil and extant lycophte spores (Tryon and Lugardon 1991) and in liverworts (Brown *et al.* 1986).

IDENTIFICATION OF SPORES AND PLANT AFFINITY

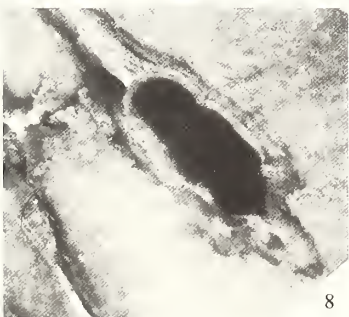
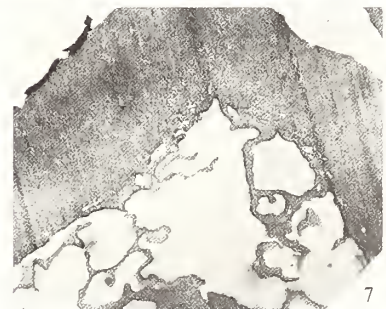
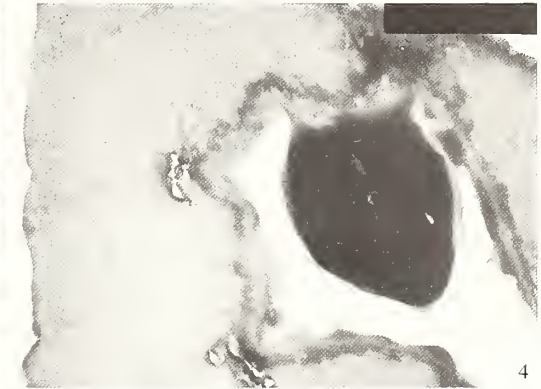
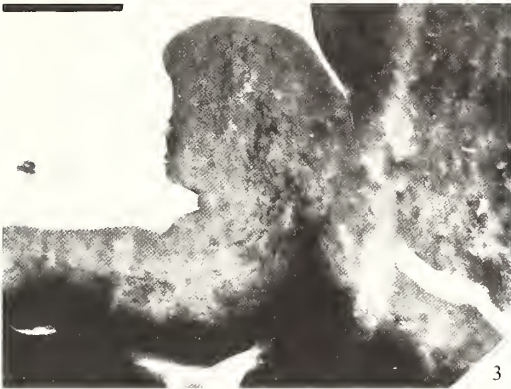
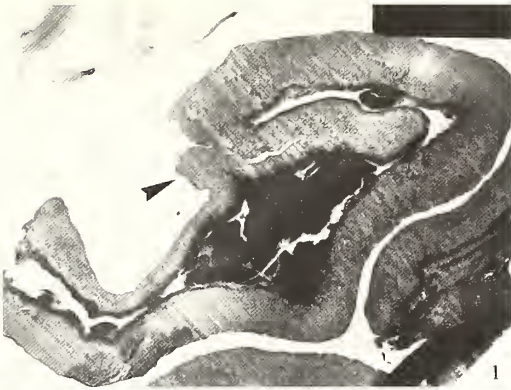
When originally describing the spores extracted from *Pertoneella dactylethra* (Fanning, Edwards and Richardson 1991), it was noted that they resembled one of the spores illustrated in the paper containing the original description of *Retusotriletes coronadus* Rodriguez Gonzalez, 1983 which

EXPLANATION OF PLATE 5

Figs 1–10. TEMs of *Retusotriletes* cf. *coronadus*; NMW95.19G.10; Perton Lane, Pridoli, Welsh Borderland.

1, almost entire spore before acid treatment, trilete fold is arrowed; $\times 5500$. 2, spore after acid treatment; trilete arrowed; note absence of dark bodies in lumen; $\times 3260$. 3, magnification of trilete fold in fig. 1; $\times 25000$. 4, area of spore, before acid treatment, showing position of lumen (light area); electron-dense body partly surrounded by narrow layer and layering to inside of the exospore; $\times 25000$. 5, proximal (light) and distal walls of same spore before acid treatment; darker staining areas around lumen may indicate layering of exospore or adpressed spore contents; note ornament on outer edge of thinner proximal wall and possible layering in exospore; $\times 28400$. 6, magnification of 5 to show ornament on the proximal surface with some indication of lamellae in the exospore; $\times 50000$. 7, part of spore after nitric acid treatment showing network in lumen (marking original position of darker bodies) which appears continuous with the rest of the exospore; innermost region of exospore below apertural fold has spongy appearance; $\times 5780$. 8, compressed lumen filled by dark body surrounded by lighter region, with layering to inside of exospore, before acid treatment; $\times 20450$. 9, ornament on proximal surface; $\times 25000$. 10, higher magnification of inner part of exospore, showing layering adjacent to lumen; $\times 43750$.

Fig. 11. TEM of *Synorisporites downtonensis* Richardson and Lister; NMW93.143G.8; Ludford Corner, Pridoli Series, Welsh Borderland; two adjacent spores of a tetrad showing fusion of proximal surfaces (arrow) and wedge-shaped equatorial region (*), after nitric acid treatment; $\times 910$.



occurs in dispersed assemblages from the Lower Devonian of Spain and is identified as *R. coronadus* in the figure legend. The *in situ* *Pertonella* spores did not exactly conform with the illustrated holotype nor to the diagnosis of that species and consequently the specific prefix 'cf.' was used in 1991.

Dispersed spores almost identical to the *in situ* spores from *P. dactylethra* are relatively common in the matrix at Perton Lane (Fanning, Edwards and Richardson 1991) and, following re-examination of the type material for *R. coronadus*, will probably be placed in a new species of *Retusotriletes* (JBR, work in progress). However, the *in situ* spores are larger (34 (39) 45 μm : 20 specimens measured), than the dispersed specimens (14 (22) 36 μm : 44 specimens measured). The spores described in this paper are almost identical to those extracted from the coalified compression fossils of *P. dactylethra* from the same locality but are smaller and are more similar in size to the dispersed examples.

In considering broad affinities, the arguments rehearsed for the *Synorisporites downtonensis* spore masses are equally relevant here, particularly as regards the lack of any peripheral material, and hence presumably perispore. However, in this case the spores are contained in sporangia that terminate naked dichotomously branching axes. In that it has not been possible to demonstrate tracheids, such plants are called rhyniophytoid, but are probably tracheophytes. Sporangial shape is identical with that of the tracheophyte *Cooksonia pertoni* and, although the sporangial spines might be considered a specific character, Fanning, Edwards and Richardson (1991) decided to place the Perton Lane fossils in a new genus because of their highly distinctive retusoid spores. These ultrastructural studies, in failing to demonstrate peripheral material or the bilayered exospores typical of *Ambitisporites* – *Synorisporites verrucatus* – *Streelispora newportensis*/*Aneurospora* in the *Cooksonia pertoni* lineage, further justify that decision. *Pertonella* is not closely related to *Cooksonia*. Absence of extrasporal layers hints at affinity with certain homosporous lycopods (Tryon and Lugardon 1991) but unfortunately there is no information on spores of approximately coeval examples (sometimes called prelycophytes) such as *Drepanophycus*, *Baragwanathia* and *Asteroxylon* (Gensel 1992; Hueber 1992; Li and Edwards 1995). In this context it is perhaps relevant that Hueber (1992) has suggested that both zosterophylls and lycophytes had their origins in a plexus of cooksonioid plants (cooksonioid here referring to sporangial shape) and that the two groups became separate somewhere between the 'late Early Silurian and the early Lower Devonian'. In this scenario the sporangial spines in *Pertonella* (a cooksonioid on Hueber's definition) provide evidence for a novel hypothesis for the evolution of the lycophyte leaf, i.e. that the enation was first produced on a sporangium and that the microphyll, a vascularized enation, eventually resulted from precocious development of such enations on vegetative axes (Bower 1935; Edwards 1993).

CONCLUSIONS

The kinds of comparisons employed here – the palaeobotanical taxonomist's equivalent of clutching at straws – emphasize the major dilemma in attempts to classify early land plants. Available characters are few and the plants so simple morphologically that homoplasy probably abounds. Our studies show that spores have some value in providing additional characters, but that their full potential will not be realized until we have more information on modern and fossil taxa (particularly bryophytes), a greater understanding of spore and sporangial development in extant forms, elucidation of the effects of diagenesis on spore ultrastructure and, of course, more fossils with *in situ* spores.

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Palaeontology

VOLUME 39 · PART 3

CONTENTS

- Systematics of the Oligocene to Miocene reef coral *Tarbellastraea* in the northern Mediterranean
ANN F. BUDD, FRANCESCA R. BOSELLINI and THOMAS A. STEMANN 515
- Architecture of the Upper Carboniferous pteridosperm frond
Macroneuropteris macrophylla
C. J. CLEAL, J.-P. LAVEINE and C. H. SHUTE 561
- The first Mesozoic Solifugae (Arachnida) from the Cretaceous of Brazil, and a redescription of Palaeozoic solifuge
PAUL A. SELDEN and WILLIAM A. SHEAR 583
- A trigonotarbid arachnid from the Upper Silurian of Shropshire
JASON A. DUNLOP 605
- A new oxytomid bivalve from the Upper Jurassic–Lower Cretaceous of Antarctica
J. A. CRAME 615
- Chitinozoa of the Silurian–Devonian boundary sections in Podolia, Ukraine
F. PARIS and Y. GRAHN 629
- Reassessment of extinction patterns among the Late Pleistocene mammals of South America
ENRIQUE P. LESSA and RICHARD A. FARIÑA 651
- A cladistic analysis of the horses of the tribe Equini
JOSÉ L. PRADO and MARÍA T. ALBERDI 663
- Two early Cretaceous spirulid coleoids of the north-western Caucasus: their shell ultrastructure and evolutionary implications
LARISA A. DOGUZHAeva 681
- Sinistral hyperstrophic coiling in a Devonian gastropod from Bohemia with an *in situ* operculum
JOHN S. PEEL and RADVAN J. HORNÝ 709
- Two *Osmundopsis* species and their sterile foliage from the Middle Jurassic of Yorkshire
JOHANNA H. A. VAN KONIJNENBURG-VAN CITTERT 719
- New observations on the ecology of the Permian Capitan reef, Texas and New Mexico
RACHEL WOOD, J. A. D. DIXON and BRENDA L. KIRKLAND 733
- Rhombopholis*, a prolacertiform reptile from the Middle Triassic of England
MICHAEL J. BENTON and ALICK D. WALKER 763
- Ultrastructure of *Synorisporites downtonensis* and *Retusotriletes* cf. *coronadus* in spore masses from the Přídolí of the Welsh Borderland
D. EDWARDS, K. L. DAVIES, J. B. RICHARDSON, C. H. WELLMAN and L. AXE 783

QE
701
P155
NH

Palaeontology

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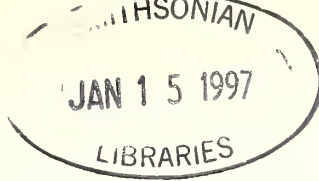
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Cover: The Middle Ordovician trilobite *Ogygiocarella* from Builth was one of the first fossils described from Britain, being figured by Edward Lhwyd in 1698.



DEDUCING THE BODY POSTURE OF EXTINCT LARGE VERTEBRATES FROM THE SHAPE OF THE VERTEBRAL COLUMN

by ANDREAS CHRISTIAN *and* HOLGER PREUSCHOFFT

ABSTRACT. Simple measurements were taken from the vertebral column of several extinct and extant terrestrial vertebrates in order to estimate the bending moments in a sagittal plane that could be sustained along the longitudinal body axis. According to theoretical expectations, the estimated patterns of sustainable bending moments prove to differ between bipeds and quadrupeds of different body proportions. In an analysis of the vertebral column of the dinosaurs *Plateosaurus* and *Iguanodon*, the former appears as a habitual quadruped, while the latter must have assumed a bipedal posture more frequently or carried most weight on the hindlimbs during quadrupedal locomotion. A separate analysis of the cross sectional areas of the vertebral centra and the lever arms of the epaxial muscles gives further information on the use of the vertebral column during locomotion and reveals aspects of the ecology of the animals under study.

EVEN if complete skeletons of an extinct species are preserved, the possible arrangements of the fossilized bones usually leave open some questions about body and limb posture. Slight changes of the relative positions of adjacent bones may summate over several joints in the limbs or in the vertebral column, so that quite different reconstructions of the same animal can be obtained. A prosauropod dinosaur, for example, may be reconstructed bipedally or quadrupedally, its limbs may appear rather sprawling or column-like and the neck might be placed nearly horizontally or more vertically (Galton 1976; van Heerden 1979; Cooper 1981; Weishampel and Westphal 1986; Christian *et al.* in press). There might be other clues like hooves on the finger tips indicating a quadrupedal body posture in some fossil vertebrates or there may be fossilized tracks that can be attributed to a particular genus with a high probability. Such fossilized tracks are not only helpful in deciding whether the track-maker was moving bipedally or quadrupedally but also in estimating the centre of mass and the gait of the animal (e.g. Alexander 1989; Thulborn 1990). However, even if such evidence is available, postures and gaits that do not fit the tracks usually cannot be excluded. A track-maker, for example, that only left tracks demonstrating quadrupedal locomotion, may have used a bipedal gait as well in situations that are not documented.

Different body and limb postures are not only associated with different arrangements of the bones, they also evoke different patterns of stresses in the skeleton (e.g. Kummer 1959; Pauwels 1965; Preuschoft 1969, 1970, 1971, 1976). If the skeletal remains of an extinct vertebrate are analysed with regard to the forces and torques that could be sustained, we can obtain further important evidence on the possible postures and gaits of this animal (Preuschoft 1976; Alexander 1985; Christian *et al.* in press).

In this study we investigate how the predominant body posture of a dinosaur (or any other terrestrial vertebrate) can be derived from the shape of the vertebral column even if the distribution of body mass is not reliably known. Based on a method similar to that developed by Preuschoft (1976) to deduce the patterns of bending moments and compressive forces in the vertebral column along the body axis, we compare the shapes of the vertebrae of several extinct and extant vertebrates that can be classified clearly as either exclusively bipedal or exclusively quadrupedal. The method is then applied to the prosauropod *Plateosaurus* and the ornithopod *Iguanodon*, the body postures of which are still the subject of controversy.

MATERIAL

Measurements were taken from vertebrae of five extant vertebrates (two mammals, two birds and one reptile) and seven dinosaurs, as listed below.

Bipeds. *Macropus giganteus* (Grey Kangaroo), SMF 53503: Senckenberg-Museum, Frankfurt, Germany (this species is included here because it is quadrupedal only at very low speeds of locomotion); *Rhea americana* (Rhea), SMF 2398: Senckenberg-Museum, Frankfurt, Germany; *Struthio camelus* (Ostrich), Institut d' Anatomie, Strasbourg, France; *Albertosaurus* (theropod dinosaur), Royal Tyrrell Museum, Canada, cast of ROM 1247, the original skeleton in the Royal Ontario Museum, Toronto, Canada; *Tarbosaurus* (theropod dinosaur), exhibition from Mongolia, touring through Germany in 1994; *Tyrannosaurus* (theropod dinosaur), exhibited cast in the Senckenberg-Museum, Frankfurt, Germany.

Quadrupeds. *Varanus salvator* (monitor lizard), ZFMK 5137A, Koenig Museum, Bonn, Germany; *Capra ibex* (Ibex), SMF 1461, Senckenberg-Museum, Frankfurt, Germany; *Dicraeosaurus* (sauropod dinosaur), exhibited specimen in the Museum für Naturkunde, Humboldt University, Berlin, Germany; *Chasmosaurus* (ceratopsian dinosaur), Royal Tyrrell Museum, Canada, from a copy of ROM 5499, the original skeleton in the Royal Ontario Museum, Toronto, Canada.

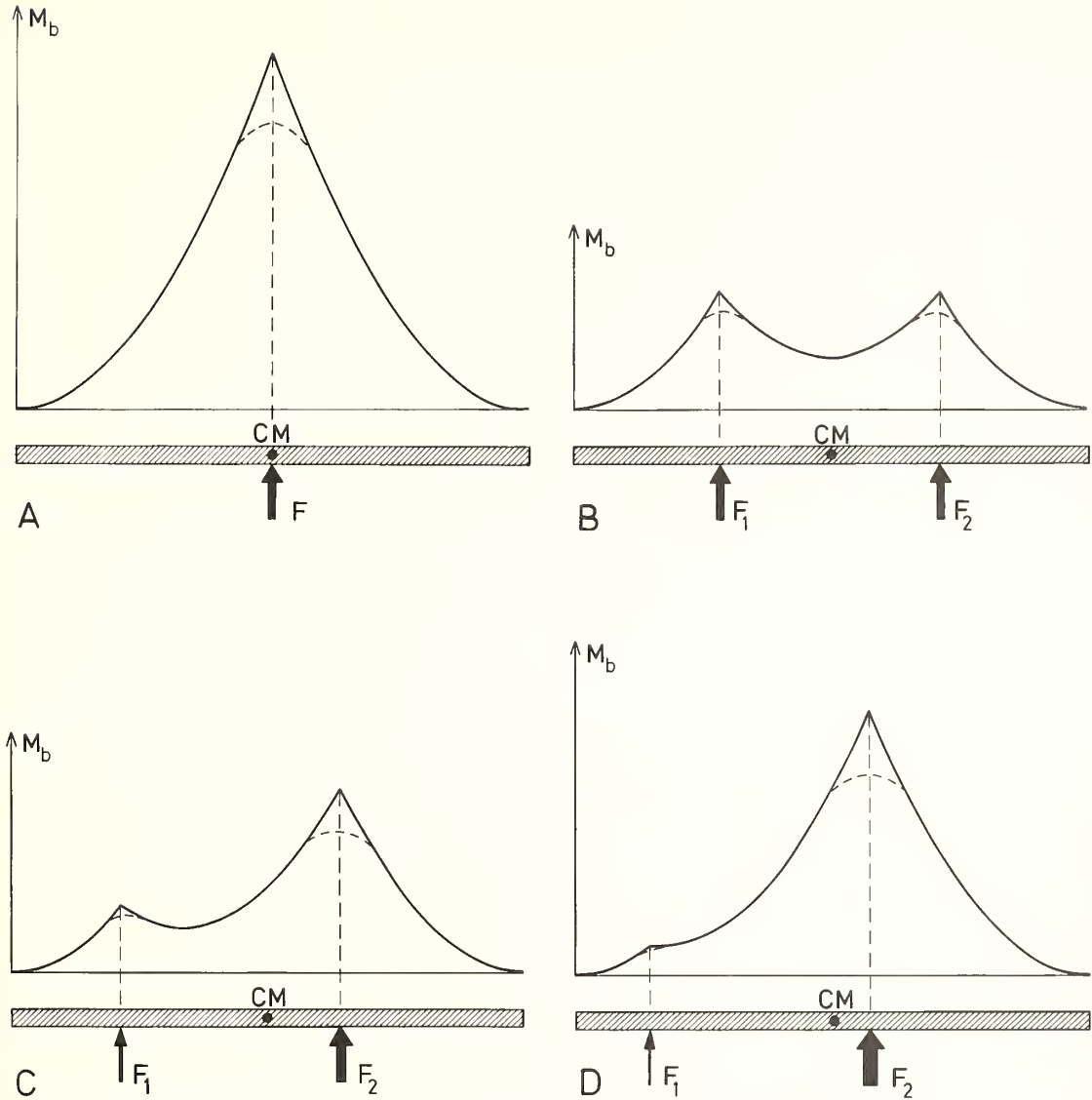
Others. *Plateosaurus* (prosauropod dinosaur), reg.-no. 1668/1, Universität Tübingen, Germany; *Iguanodon bernissartensis* (ornithopod dinosaur), exhibited cast in The Natural History Museum, London.

BENDING MOMENTS, POSTURE AND MASS DISTRIBUTION

Depending on posture and distribution of body mass, the neck, trunk and tail of a resting animal experience forces and torques (bending moments). Bending moments along the longitudinal body axis act primarily in a sagittal plane unless parts of the body, e.g. the tail, are accelerated quickly sideways.

The pattern of bending moments along the vertebral column is distinctively different between quadrupedal and bipedal animals as demonstrated schematically in Text-figure 1. In side view, a bipedal animal can be simplified as a beam carried by one pillar, a quadrupedal animal as a beam carried by two pillars. The bending moments M_b can then be calculated according to the rules of statics (e.g. Pauwels 1965). In a biped (Text-fig. 1A), the bending moments will be maximal at the hips and drop towards both the cranial and the caudal end of the body. The bending moments are considerably higher at the middle of the trunk (midpoint between hips and shoulders) than they are at the shoulders. In a quadruped (Text-fig. 1B–D), on the other hand, there will be two peaks in the curve of bending moments along the vertebral column, one at the hips and one at the shoulders. Between shoulders and hips, the bending moments will decrease and, depending on the distribution of body mass, may reach an opposite direction approximately at the middle of the trunk, thereby changing from hogging moments, which tend to bend the body convex at the dorsal surface, to sagging moments, which tend to bend the body concave at the dorsal surface. The point of minimal hogging (or maximal sagging) moments can be located close to one pair of limbs if the other pair of limbs carries most of the body weight (Text-fig. 1C–D). With an extremely small share of body weight carried by one pair of limbs, or if shoulders and hips are located close together compared to total body length, there might be only a slight drop or even no drop at all in the hogging moments between shoulders and hips (Text-fig. 1D), so that the pattern of bending moments resembles that of a biped.

If the feet are not placed below the shoulder or hip joints, respectively, vertical ground reaction forces will induce torques about these joints. Then muscles at these joints have to become active



TEXT-FIG. 1. Bending moments M_b in the sagittal plane along a homogeneous beam with a constant cross section. In A the beam is carried by one support; in B-D the beam is carried by two supports. The weight is carried equally by both supports in B and shifted towards the right from B to D. F , F_1 and F_2 are the reaction forces that are exerted by the supports on the beam.

which pulls the trunk up- or downwards, thereby increasing the bending moments between the proximal joint of the extremity and the area where the muscle force is transmitted to the trunk. Such muscle activities, however, will not change the general differences in the patterns of bending moments between quadrupeds and bipeds as described above. The well-developed pelvic girdle and, if present, a well-developed pectoral girdle, sternum and ribs distribute the forces transmitted by the limbs over a certain area and may take over some of the bending moments, so that the peaks in the curve of bending moments will be blunted (Preuschoft 1976; Alexander 1985; Preuschoft and Günther 1994). The reduction of the bending moments at hips and shoulders is indicated by the

broken lines in Text-figure 1, which are more realistic than the unbroken lines for the bending moments along the trunk axis of dinosaurs and many other vertebrates.

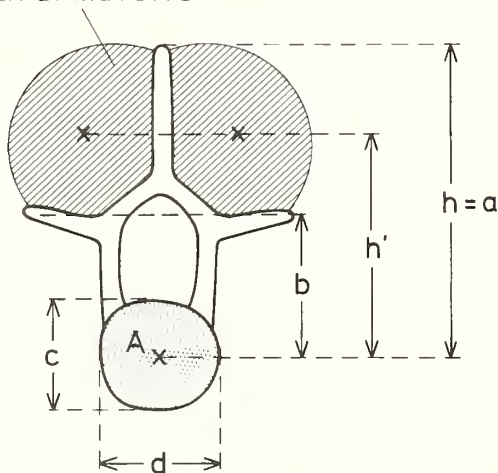
The highest forces and moments acting on an animal do not occur during rest but in fast locomotion (e.g. Alexander 1982, p. 81; Preuschoft 1989; Christian 1995). During fast locomotion, we have to take into account forces due to inertia and the fact that not all feet are placed on the ground simultaneously. Besides, the position of the feet relative to the proximal joints of the extremities change during a stride, as well as the direction and the magnitude of the ground reaction forces, and to a lesser degree also the shape and spatial orientation of the trunk (e.g. Preuschoft and Fritz 1977; Preuschoft and Günther 1994). If, however, the highest bending moments that occur during a complete cycle are calculated for each position along the trunk, we will still get a pattern that does not deviate essentially from what has been found at rest (see Preuschoft and Fritz (1977) for a detailed analysis of the bending moments along the trunk axis of a horse during locomotion). It should be mentioned that our analysis cannot be applied without further examination on animals that do not experience the highest forces and torques during terrestrial locomotion on firm ground.

VERTEBRAL SHAPE AND THE PATTERN OF BENDING MOMENTS

Sagging bending moments, which may occur in the middle of the trunk of some quadrupedal vertebrates (see above), can be counteracted by tension in abdominal muscles and compressive forces in the vertebral column. More important for our analysis are hogging bending moments.

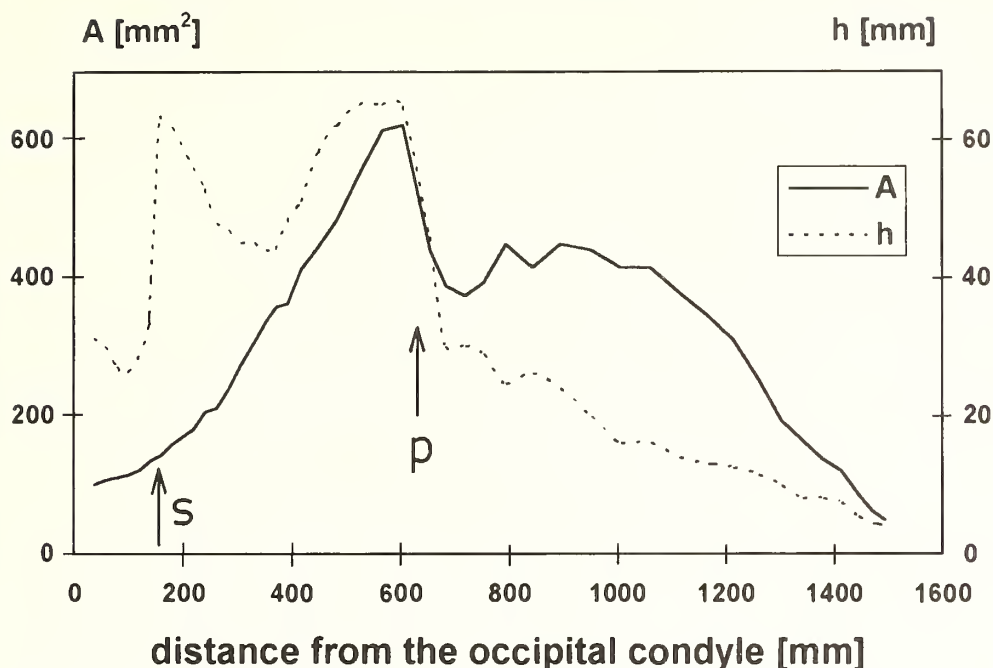
Hogging bending moments must be counteracted at the intervertebral junctions by tension in epaxial muscles which are supported by ligaments that connect the spinal processes (Text-fig. 2; see

epaxial muscles



TEXT-FIG. 2. Schematic caudal view of a vertebra. The measurements a , b , c and d were taken to calculate the lever arm of the epaxial muscles and the cross sectional area A of the vertebral centrum, as explained in the text. h : lever arm estimated according to Alexander (1985), h' : lever arm estimated according to Preuschoft (1976).

also Preuschoft 1976; Alexander 1985, 1989). A muscle force F acting in a sagittal plane at a distance h above the transverse axis of an intervertebral joint produces a torque $F \times h$ about that joint; h is the lever arm of the force F . The lever arm is the distance between the line of action of the force and the axis of the joint. The torque can be increased by either increasing the force, the lever arm, or both. The transverse axis of an intervertebral joint can be assumed to pass through the centre of the intervertebral disc (Preuschoft 1976; Alexander 1985). The lever arms of the epaxial muscles can be estimated from the shape of the vertebrae. Preuschoft (1976) assumed h to be equal to the vertical distance between the centre of the epaxial muscles and the centre of the intervertebral discs. He suggested that h be estimated to be equal to $(a + b)/2$ with a the distance from the midpoint of the vertebral centrum (vertebral body) to the tip of the spinal process and b the distance

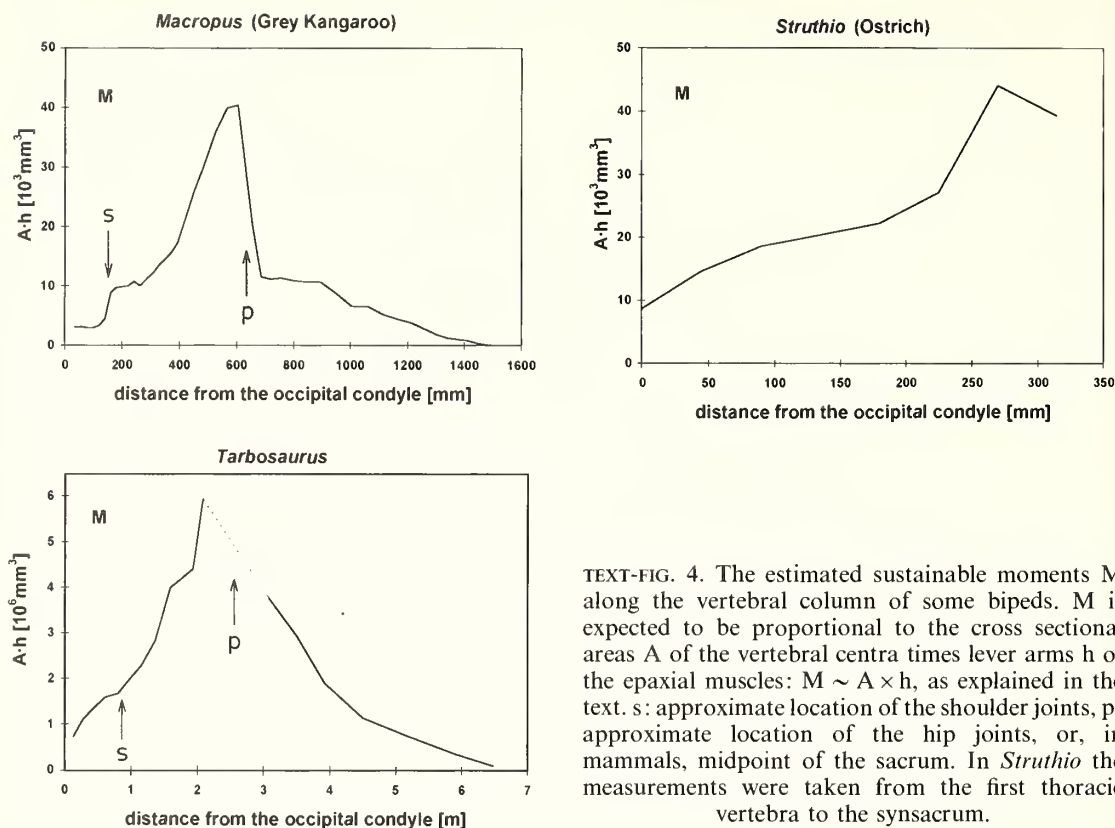


TEXT-FIG. 3. Lever arms h of the epaxial muscles and cross sectional areas A of the vertebral centra along the vertebral column of *Macropus giganteus* (Grey Kangaroo). s : approximate location of the shoulder joints, p : pelvis, midpoint of the sacrum.

from the midpoint of the vertebral centrum to the bases of the transverse processes (see Text-fig. 2). For some dinosaurs, Alexander (1985) found it more likely that the muscle force F was transmitted mainly by tendons close to the tips of the spinal processes. He estimated h to be equal to a . For our purpose, both methods lead to similar results (see below). Further problems in estimating h arise if epaxial muscles or their tendons are located far above the spinal processes. This is unlikely in the trunk but quite common in the necks of mammals (e.g. Preuschoft and Fritz 1977; Preuschoft and Günther 1994).

The maximum muscle force F at a given position in the vertebral column seems to be difficult to obtain, because the functional cross section of the epaxial muscles cannot be deduced from skeletal remains. Preuschoft (1976), however, pointed out, that the pulling force F of the epaxial muscles evokes a compressive force of the same magnitude between the vertebral centra. Therefore, under the assumption of equal safety-factors along the vertebral column, the highest regularly occurring forces F should be proportional to the transversal cross sections of the centra or of the intervertebral discs. The cross sections A of the intervertebral discs may be the better measure for the compressive forces and can be assumed to be approximately equal to the surface areas of the adjacent vertebral centra (Preuschoft 1976). It has been argued that bending moments could also be counteracted by elevated pressure in the body cavity (Preuschoft *et al.* 1979; Alexander and Jayes 1981). Alexander (1985), however, stated that for dinosaurs such elevated pressure could not be maintained while breathing in. Anyway, if elevated pressure in the body cavity takes over a fraction of the compressive forces, this fraction will be similar between shoulder and hip joint and therefore not affect much the general pattern of compressive forces acting along the vertebral column of the trunk.

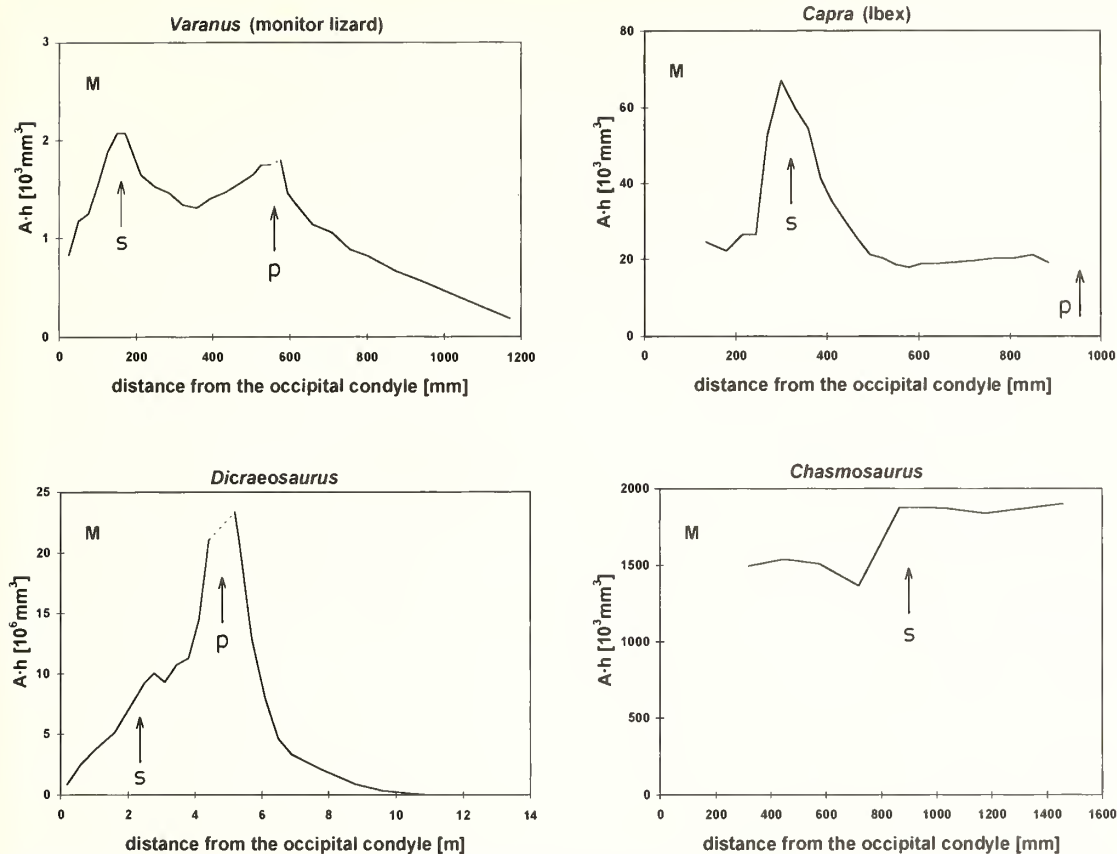
To calculate A and h , the length measurements a , b , c and d , as defined in Text-figure 2, were taken with calipers at the caudal end of the vertebrae. The area of the caudal surface of each



TEXT-FIG. 4. The estimated sustainable moments M along the vertebral column of some bipeds. M is expected to be proportional to the cross sectional areas A of the vertebral centra times lever arms h of the epaxial muscles: $M \sim A \times h$, as explained in the text. s : approximate location of the shoulder joints, p : approximate location of the hip joints, or, in mammals, midpoint of the sacrum. In *Struthio* the measurements were taken from the first thoracic vertebra to the synsacrum.

centrum was calculated by assuming an elliptical shape with c and d as major axes. In the thoracic region, compressive forces between adjacent centra can be exchanged partly by the heads of the ribs. If the surface areas of the rib articulations at the caudal end of a vertebra were not negligibly small, they were added to the caudal surface area of the centrum to obtain A . Distances from the occipital condyle were measured with a tape ventrally along the vertebral centra. A was multiplied by h to obtain a measure for the moment M that can be produced by the epaxial muscles at a given location of the vertebral column. M is equivalent to the highest sustainable (hogging) bending moment. The distribution of h and M along the vertebral column differed only slightly between the two methods of estimating the lever arms of the epaxial muscles. Therefore, we present only the data with h estimated to be equal to the distance between the midpoint of the vertebral centrum and the tip of the spinal process.

Because of the reciprocal interdependence of lever arms of muscles and compressive forces in the vertebral column, there are always two possibilities in each animal: the lever arms may correlate either with the pattern of bending moments, or with the cross sectional areas. Both may be true and are mechanically equivalent. The data of Preuschoft (1976) on *Diplodocus* and Alexander (1985) on *Diplodocus* and *Iguanodon* as well as our own data on most of the animals studied here are in accordance with the assumption that the pattern of bending moments is already reflected in the lever arms of the epaxial muscles along the vertebral column. Some data like those on *Macropus* (Text-fig. 3), however, are clearly contradictory, demonstrating that the patterns of h and A can be quite different. We therefore prefer to use the full information of lever arms and cross sectional areas to estimate the sustainable bending moments.



TEXT-FIG. 5. The estimated sustainable moments M along the vertebral column in selected quadrupeds. Explanations as in Text-figure 4.

BIPEDS AND QUADRUPEDS COMPARED

Bipeds. In all bipeds examined in this study, the moment M reaches its maximum at the hips and drops continuously towards both ends of the body with no local maximum or plateau at the shoulders (Text-fig. 4). The general pattern of the estimated moments M is similar in the three theropods so that only the data for *Tarbosaurus* are presented, although M decreases more towards the head in this species, especially if compared with *Albertosaurus*. The data for *Rhea* are not presented either, because they are very similar to those of *Struthio* (as well as additional data for other ratites). In *Macropus*, in the neck and at the base of the tail h is underestimated, because in these areas some tendons and muscles are located far away from the spinal processes of the vertebrae as in the neck of many other mammals, e.g. horses. In fossils, we usually can only guess whether there were ligaments or muscles present above the spinal processes. This, however, is very uncommon in the vertebral column between shoulders and hips of all extant vertebrates and, in view of the usually high spinal processes in this section, is unlikely in most dinosaurs.

Quadrupeds. In Text-figure 5 the patterns of the estimated moments M along the body axis are plotted for all quadrupeds studied here. A recalculation of the data for *Diplodocus* presented by Preuschoft (1976) gives results very similar to those for *Dicraeosaurus*.

In all specimens, the pattern of M is in accordance with our expectations. Around the shoulders, there is always a local maximum or at least a plateau visible. The pattern in the monitor lizard is

similar to that given in Text-figure 1b with two distinct peaks of M of roughly similar size at the shoulders and hips. In the monitor, however, the tail is longer and heavier than head and neck, so that we would expect a higher local maximum at the hips than at the shoulders. Therefore, the pattern of bending moments, if derived from the actual distribution of body mass, is rather similar to the pattern given in Text-figure 1c. The relatively higher moments M that can be sustained at neck and shoulders might be due to activities other than locomotion. The monitor is a predator which sometimes uses strong movements of head and neck while killing prey.

In the sauropods, there is only a slight reduction of M between shoulders and hips below the values found at the pectoral girdle. This is in accordance with our expectation for animals with well-developed pectoral girdles that distribute the loads transmitted through the shoulder joints over a long section of the trunk, and which carry much more weight on the hindlimbs than on the forelimbs, as illustrated in Text-figure 1d (see also Preuschoft (1976) and Alexander (1985) for the statics of *Diplodocus*). The location of the more cranial maximum in the pattern of M behind the shoulders instead of directly at the shoulders leads to the conclusion that either the shoulder joints were located more caudally than in the reconstructions used for our measurements or that the forefeet were placed behind the shoulder joint. Another possible explanation of the data would be to invoke tendons or ligaments far away from the spinal processes in the shoulder region. This latter possibility, however, seems rather improbable in view of the high spinal processes in this region, as mentioned before.

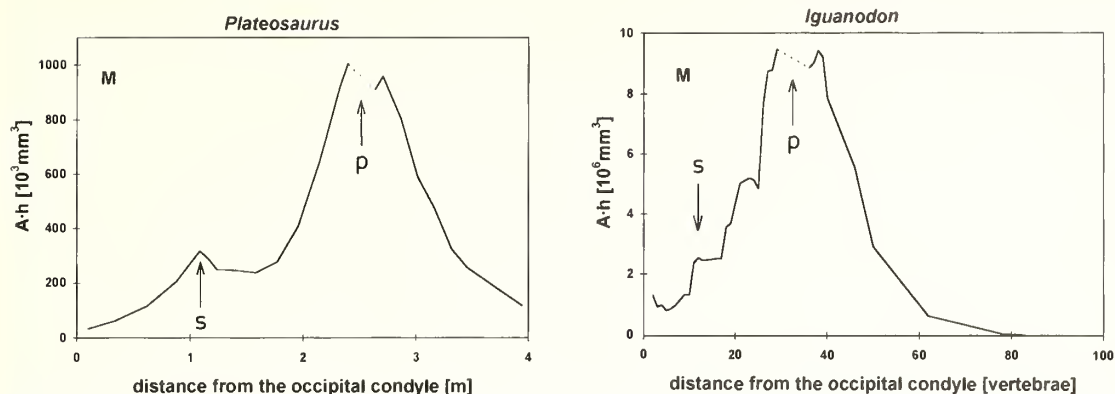
The situation is reversed in *Capra*, which has a long neck and a very short and light tail so that no peak of the moments occurs at the hips, provided the animal stands with the hindlimbs more or less perpendicular.

The data from the vertebral column of *Chasmosaurus* (Text-fig. 5) are problematical for our analysis, because its armour indicates that activities other than locomotion might have been the primary factors for the shaping of the vertebral column (see below). Furthermore, the expanded pectoral girdle may have distributed the forces transmitted by the forelimbs over such a long section that there was no clear maximum of the bending moments close to the shoulders. Nevertheless, the estimated moment M is about constant from the base of the neck to the middle of the trunk in *Chasmosaurus*, in accordance with our expectations for the pattern of bending moments in a quadruped with a well-developed pectoral girdle, and distinctively different from all the examined bipeds in which M decreases continuously from the sacrum towards the shoulders.

Plateosaurus and *Iguanodon*. As mentioned before, the body posture of *Plateosaurus*, as well as of other prosauropods, is not reliably known (Galton 1976; van Heerden 1979; Weishampel and Westphal 1986; Christian *et al.* in press). Individuals in museums are placed sometimes in quadrupedal and sometimes in bipedal postures. It is possible that *Plateosaurus*, like many modern lizards (Christian *et al.* 1994a, 1994b; Christian 1995), became bipedal at high speeds, being otherwise quadrupedal. Some fossil tracks of bipeds have been attributed to prosauropods, but this interpretation has been questioned (see Thulborn 1990, p. 176, for a detailed analysis of fossil prosauropod tracks).

The pattern of M along the vertebral column in *Plateosaurus* shows two distinct local maxima at shoulders and hips (Text-fig. 6). The peak at the hips is much higher than the peak at the shoulders. The moments evidently have been rather low along the whole length of the neck. These observations are consistent with a quadrupedal body posture and a more or less vertical neck posture. A bipedal posture may have been assumed occasionally but the data do not fit a habitually bipedal posture. *Plateosaurus*, therefore, appears to have been a habitual quadruped, which may have used a bipedal gait infrequently at its fastest locomotion, or during standing.

For *Iguanodon*, some evidence from tracks and from the skeleton indicate that this dinosaur used a quadrupedal gait at low speeds and a bipedal gait at high speeds of locomotion (Currie and Sarjeant 1979; Norman 1986; Norman and Weishampel 1990; Thulborn 1990, p. 190). The vertebrae of *Iguanodon* available for this study are in a less well-preserved condition than those of *Plateosaurus*, so that the curve of M is less smooth (Text-fig. 6). The pattern of the moment M ,



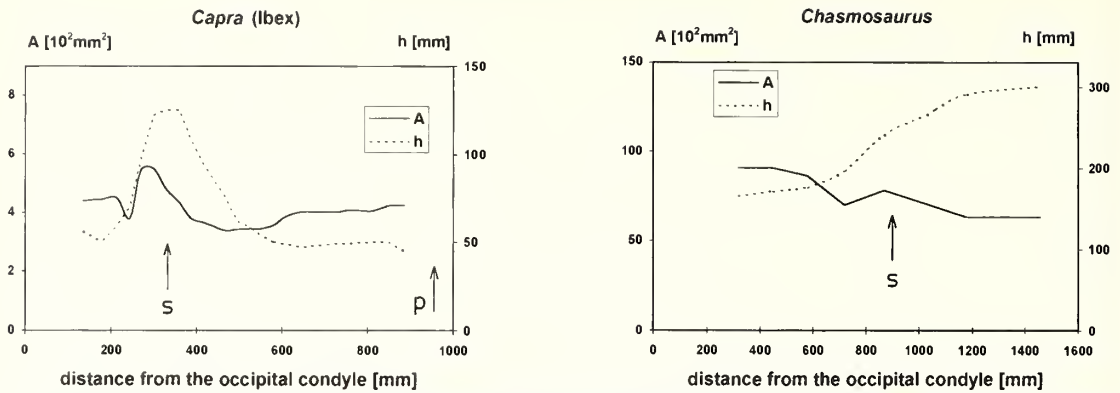
TEXT-FIG. 6. The estimated sustainable moments M along the vertebral column of *Plateosaurus* and *Iguanodon*. Explanations as in Text-figure 4.

however, has only one pronounced peak at the hips. Towards the head M decreases continuously, though there might be a plateau or a much less pronounced second peak at the shoulders. The overall pattern of bending moments along the body axis is very similar to that of *Macropus* (Text-fig. 4), which is also very similar to *Iguanodon* in its overall body proportions. Therefore, the data for *Iguanodon* are in accordance to a frequent use of a bipedal body posture especially during fast locomotion and a quadrupedal posture which was used only at slow speeds as in kangaroos. The plateau or low local maximum of the bending moments at the shoulders might indicate a minor shaping influence of the quadrupedal posture that was probably assumed at low speeds, as in kangaroos. A quadrupedal posture at high speeds of locomotion is only in accordance with the data if very little weight was carried by the forelimbs.

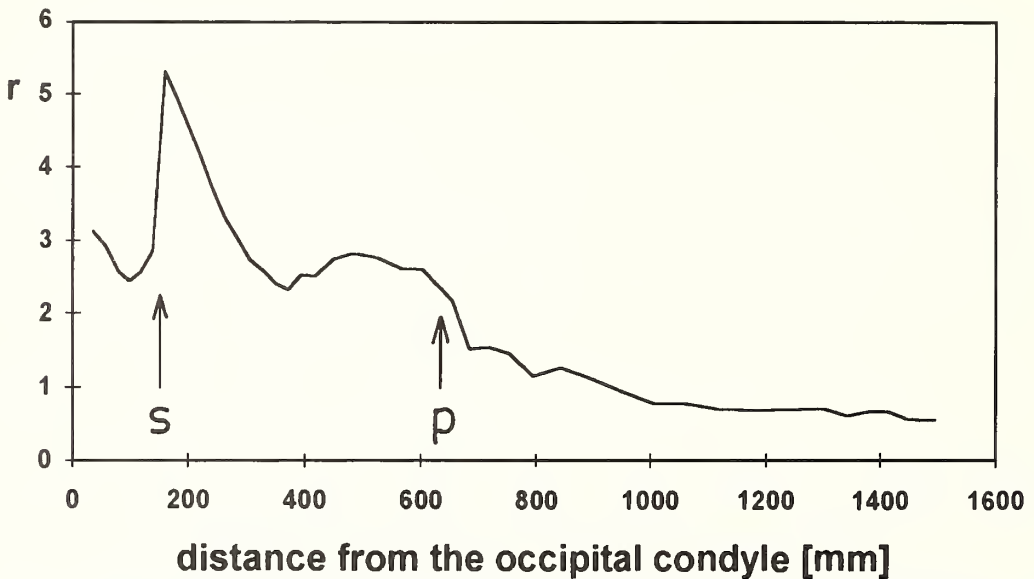
ADDITIONAL INFORMATION ABOUT LIFE-STYLE

For extinct animals, assessments of the distribution of body mass are usually highly speculative. In our approach to determine the body posture from the shape of the vertebral column, we do not need much knowledge about the distribution of body mass of the examined animals. If, on the other hand, a reasonable and reliable model of an animal is available, a reconstruction of the pattern of bending moments along the vertebral axis may allow a reconstruction of the posture of neck and tail, as well, as demonstrated by Preuschoft (1976) for *Diplodocus* and mentioned above for the neck posture of *Plateosaurus*. The neck and tail of vertebrates, however, are often involved in activities other than locomotion, so that in some animals they might be much stronger than necessary to cope with regular forces and torques during locomotion, as discussed above for *Varanus*. In goats and probably also in ceratopsians like *Chasmosaurus* the heads are utilized in strenuous ritual combat (Farlow and Dodson 1975; Alexander 1989, p. 73; Dodson and Currie 1990). Accordingly, the sustainable moments M are relatively high in the necks of *Capra* and *Chasmosaurus* (Text-figs 4–5). Especially in the distribution of the cross sections A of the vertebral centra in the neck and at the shoulders, a characteristic situation is found in both species (Text-fig. 7). The cross sections A decrease towards the head in all other animals studied here except in these two species in which A is about constant between shoulders and head (*Capra*) or increases slightly towards the head (*Chasmosaurus*). This is to be expected in association with the high compressive forces in the cervical spine during the head-to-head fighting undertaken by goats.

The relatively high estimates for the moments at neck and shoulders in *Albertosaurus* compared with the other theropods studied here, especially *Tarbosaurus*, might result from differences in the distribution of body mass of the theropods examined; alternatively, it might indicate an involvement of trunk and neck in more strenuous activities in *Albertosaurus*, such as the killing of



TEXT-FIG. 7. Lever arms h of the epaxial muscles and cross sectional areas A of the vertebral centra along the vertebral column of *Capra ibex* (Ibex) and *Chasmosaurus*.



TEXT-FIG. 8. The ratio r between the lever arm h of the epaxial muscles and the cross sectional area A of the vertebral centra along the vertebral column of *Macropus giganteus* (Grey Kangaroo).

large prey. For a conclusive analysis, however, reliable estimates of the distribution of body mass in the three species, and data from the vertebral columns of several individuals of each species would be necessary.

As mentioned above, a particular torque can be produced either by a high force and a short lever arm, or by a low force and long lever arm. The first solution permits rapid movements, the second solution is not adequate for rapid movements but permits stabilization of the joint with little force and energy expense. Therefore, comparing h and A , as measures for lever arm and force, respectively, provides additional information on the mechanics of the longitudinal body axis.

In *Macropus*, for example, head and neck are held in a relatively fixed position during locomotion, while tail and lumbar region are very active during hopping. Accordingly, A remains high in the proximal part of the tail, where the vertebral column is compressed by muscles that move the tail, while A drops quickly from the sacrum towards the head (Text-fig. 3). The lever arms are

long at the shoulders, thereby allowing economical stabilization of the neck during locomotion. For a quantitative comparison of lever arms and forces that can also be used across species, we might use the dimensionless ratio r , which is h divided by the square root of A . The ratio r should be high in regions of the vertical column that are not involved in rapid movements in a sagittal plane. The reverse ratio $1/r$ might be used as a measure for 'agility'. In Text-figure 8, r is plotted along the vertebral column of *Macropus*, further illustrating the analysis given above. The ratio r is high in the thorax but much lower everywhere else, especially in the tail, which is not only flexed and extended periodically during locomotion but also used actively to balance the body.

(Semi)bipedal ornithopods usually have long lever arms h of the epaxial muscles especially around the hips (e.g. Norman 1986; Norman and Weishampel 1990) where the highest bending moments occur, so that tail and trunk could be kept straight with little force and low energy expenditure. Similar-sized theropods, on the other hand, tend to have shorter lever arms, but higher cross sectional areas of the vertebral centra, indicating that the vertebral column was involved in forcefully performed rapid movements such as might have occurred during predation. Along the trunk, the average ratio r of the lever arm h divided by the square root of A is about 2.2 for *Tarbosaurus* and *Albertosaurus*, about 2.9 for *Tyrannosaurus* and between 3.0 and 3.5 for *Iguanodon*. At the base of the tail, r is about 2, or slightly higher, in *Tarbosaurus* and around 3 in *Iguanodon*. In the light of these results, *Albertosaurus* appears as a ferocious predator, well suited for killing large as well as agile prey by rapid and forceful attacks with its head.

CONCLUSIONS

We conclude that the shape of the vertebral column reflects body posture. The bending moments which can be resisted by neck, trunk, and tail can be described sufficiently with simple measurements taken from a sufficient number of vertebrae. The pattern of bending moments along the longitudinal body axis is determined by mass distribution and body posture. Because of their relationship, it is possible to predict one variable if the others are known, or are estimated independently. In particular, we can distinguish between habitual or exclusive bipeds and habitual or exclusive quadrupeds mainly by looking at the vertebral column between shoulders and hips. Because of the marked differences between the patterns of bending moments in bipeds and quadrupeds respectively, we usually do not need much more information than the shape of the vertebral column to distinguish between these basically different body postures. A more detailed picture of the body posture of a dinosaur, which includes, for example, the posture of the neck, can be drawn if reliable information about the distribution of body mass is available. With a more sophisticated approach, including separate analyses of lever arms of epaxial muscles and cross sections of vertebral centra, it is possible to provide a new evidence not only on the posture of a dinosaur but also on how it moved, or what it did with its head and neck.

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LAMNIFORM SHARKS OF THE MID CRETACEOUS ALINGA FORMATION AND BEEDAGONG CLAYSTONE, WESTERN AUSTRALIA

by MIKAEL SIVERSON

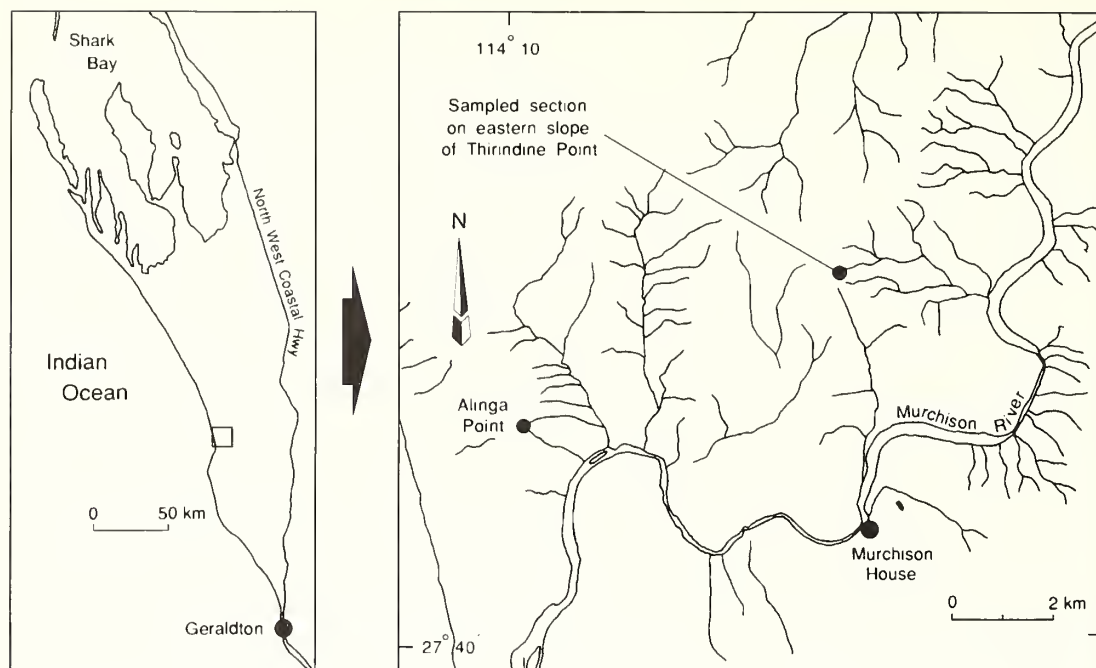
ABSTRACT. The uppermost beds of the Alinga Formation and the basal part of the overlying Beedagong Claystone in the lower Murchison River area at the southern end of the Southern Carnarvon Basin, Western Australia, have yielded 15 species of lamniform sharks referred to ten genera, of which one genus and three species are new: *Cretoxyrhina mantelli*, *Archaeolamna* aff. *kopingensis*, *A. haigi* sp. nov., *Leptostyrax* sp., *Cretolamna appendiculata*, *C. gunsoni* sp. nov., *Pseudoisurus tomosus*, *Pseudoisurus*? sp., *Paranomotodon* sp., 'Anomotodon' sp., *Johnlongia allocotodon* gen. et sp. nov., *Carcharias* sp. A, *C.* sp. B, *Squalicorax* ex gr. *curvatus*, and *S. volgensis*. Direct correlation with Germany and the Saratov Province of the Russian Platform, using cosmopolitan lamnoids, dates the basal part of the Beedagong Claystone in the studied area as early or mid Cenomanian. The top of the Alinga Formation is provisionally placed in the early Cenomanian. This contrasts with the most recent previous estimate which suggested an early Turonian age for the upper half of the Alinga Formation. The present account is the first comprehensive documentation of Cretaceous selachians from Australia. It demonstrates the great potential of the use of lamniform shark teeth in intercontinental correlation of mid Cretaceous marine deposits.

TOOTH morphology is an important character for taxonomists working on extant sharks (Bass 1973; Compagno 1984; Last and Stevens 1994). All living species of the order Lamniformes can be identified by their dentition alone (see Compagno 1984) and most of them have a very wide distribution, with reported occurrences in both the southern and northern hemispheres. In this paper, the uppermost beds of the Alinga Formation and the basal part of the overlying Beedagong Claystone are placed in an international stratigraphical framework on the basis of teeth of cosmopolitan lamnoid sharks, allowing direct correlation with north-west Germany and the Saratov Province of the Russian Platform.

As pointed out by Kemp (1991), little work has been done on Australian Cretaceous chondrichthyans. This is the first comprehensive description of Cretaceous sharks of Australia. One new genus and three new species are described: *Archaeolamna haigi* sp. nov. and *Cretolamna gunsoni* sp. nov. of the Cretoxyrhinidae Glikman, 1958 and *Johnlongia allocotodon* gen. et sp. nov., assigned to the Odontaspidae Müller and Henle, 1839.

GEOLOGY

In the onshore part of the Southern Carnarvon Basin (basin nomenclature of Hocking *et al.* 1994), south of Shark Bay, the Alinga Formation (named by Clarke and Teichert 1948; amended by Johnstone *et al.* 1958) forms the uppermost unit of the siliciclastic Winning Group ('Winning Series' of Raggatt 1936; amended by Fairbridge 1953 and Johnstone *et al.* 1958). The formation comprises a 3–22 m thick marine sequence of dark green greensand, clayey siltstone and silty claystone (Hocking *et al.* 1987). It crops out mainly in the lower Murchison River area, at the southern end of the Southern Carnarvon Basin, where it rests conformably on the late Aptian to early Albian Windalia Radiolarite (see Ellis 1993) and, at most localities, is succeeded



TEXT-FIG. 1. Map of the lower Murchison River area, Western Australia, showing the location of the sampled section on the eastern slope of Thirindine Point.

disconformably by the Toolonga Calcilutite of Santonian to early Campanian age (Belford 1958). However, in places, a thin sequence of the Beedagong Claystone is present between the Alinga Formation and the Toolonga Calcilutite. This lithostratigraphical unit was introduced formally by Shafik (1990) for a calcareous claystone between the Gearle Siltstone, which is a thicker lateral equivalent of the Alinga Formation (Condon 1968), and the Toolonga Calcilutite farther north in the Exmouth Sub-basin of the Northern Carnarvon Basin. Shafik (1990) assigned a late Turonian to late Coniacian age to the 83 m thick type section of the Beedagong Claystone in the Rough Range South #1 well, near Exmouth. This contrasts somewhat with Belford and Scheibnerova's (1971) study of planktic Foraminifera. They gave an early Turonian age for a sample from about 10 m above the base of the type Beedagong (core log 68). Until now, the Beedagong Claystone was not known to crop out in the lower Murchison River area.

PREVIOUS WORK ON THE ALINGA FORMATION

Due to the assumed absence of age-diagnostic fossils, Clarke and Teichert (1948) did not specifically discuss the age of their new lithostratigraphical unit, the Alinga Beds (= Alinga Formation of Johnstone *et al.* 1958), but it is quite clear from their discussion that they believed it to be of Late Cretaceous age. Moreover, their finds of *Marsupites* Miller, 1821 and *Uintacrinus* Grinnel, 1876 in the overlying Toolonga Chalk (= lower half of the Toolonga Calcilutite of Johnstone *et al.* 1958) further constrained the presumed age of the Alinga Beds to within the Cenomanian to Santonian interval. The only fossils from the Alinga Formation reported by Clarke and Teichert were belemnite guards.

Johnstone *et al.* (1958) gave a brief description of the type section at Alinga Point (Text-fig. 1). They correlated the formation with the Gearle Siltstone (*sensu* Condon *et al.* 1956) and concluded

that it was Albian to Cenomanian in age based on an unspecified microfauna. McWhae *et al.* (1958) favoured a correlation with part of the Gearle Siltstone but admitted that the Albian to early Turonian age assigned by them to the Alinga Formation had not yet been verified by fossils. As well as belemnites, they also reported radiolarians and fish remains. A probable Cenomanian to early Turonian age was advocated by Belford (1958), yet again an estimate unsupported by age-diagnostic fossils.

Edgell's (1964) description of his Lancelin Beds in the Perth Basin also included a table showing, but not explaining, his view on the correlation of the Cretaceous formations of the Carnarvon and Perth basins. Instead of correlating the Alinga Formation with the Gearle Siltstone, he considered the former to be considerably younger, approximately spanning the late Coniacian to mid Santonian.

Playford *et al.* (1975) did not add any new information but were of the opinion that the Alinga Formation may be Albian to Turonian in age. Likewise, Hocking *et al.* (1987) concluded that the stratigraphical position of the unit suggests that it is Albian to Turonian in age. They also stated that the formation yields radiolarians, foraminifers, belemnites, and microscopic fish teeth but that none of these groups is abundant nor has any been studied. However, at least some work has been undertaken on the belemnites, with Stevens (1965) recording *Dimitobelus diptychus* from the Alinga Point section.

In a work devoted to the Upper Cretaceous nannofossils of the Australian western margin, Shafik (1990) recorded some poorly preserved coccoliths from two beds in the upper half of the formation at Toolonga Point. On the basis of these he referred this part of the unit to the early Turonian.

MATERIALS AND METHODS

Surface-collecting confined to the uppermost metre of the Alinga Formation and the basal part of the Beedagong Claystone along the Thirindine Point ridge yielded 122 determinable teeth from lamniform sharks. In addition, two horizons of the Beedagong Claystone on the eastern slope of the Thirindine Point ridge were targeted for bulk sampling. A total of 158 kg (dry weight) was processed. The sediments were dried, then soaked in water for an hour before being gently sieved through a 330 μm mesh. When necessary, the residue was further soaked in water to which had been added automatic-washing-machine powder. Subsequent wet-sieving completely disaggregated the remaining matrix, leaving a clean residue comprising selachian teeth and dermal denticles, various skeletal remains of bony fishes, coprolites, rare phosphatic brachiopods, and glauconite. The two samples, picked down to 500 μm , yielded 324 teeth of lamniform sharks, as well as several thousand teeth of other selachians that will be described elsewhere.

AGE OF THE ALINGA-BEEDAGONG TRANSITIONAL BEDS

Thirindine Point section

At the Thirindine Point ridge (Text-fig. 1), the Beedagong Claystone is separated from the overlying Toolonga Calcilitite by a bed of elongated and irregularly shaped phosphatic nodules. On the eastern slope of the ridge, the Beedagong Claystone does not exceed about 0.5 m in thickness. *Chondrites*-bioturbated laminae, littered with glauconite grains and fish debris, occur abundantly in the lower part and are especially densely packed in the basal 20 mm which separates it from the underlying greenish clayey siltstones of the Alinga Formation. On the western slope of the ridge the Beedagong is thicker, reaching approximately one metre. Preliminary bulk sampling of the uppermost metre of the Alinga Formation, which is about 6 m thick at Thirindine Point, has revealed selachian faunas completely different in composition from that of the basal Beedagong Claystone, demonstrating a profound shift in palaeoenvironment.

STAGE	AMMONITE		RANGE OF SELACHIANS	RANGE OF BELEMNITES	BELEMNITE ZONES	
	ZONES	SUBZONES			NW EUROPE	RUSSIAN PLATFORM
CENOMANIAN	LATE	<i>Neocardioceras juddii</i>	<i>Squalicorax volgensis</i>	NW Europe		
		<i>Metoicoceras geslinianum</i>			<i>A. plenus</i>	
		<i>Calycoceras guerangeri</i>				<i>A. plenus</i>
	MIDDLE	<i>Acanthoceras jukesbrownei</i>		<i>A. primus</i>		
		<i>Acanthoceras rhotomagense</i>				
		<i>Turrilites acutus</i>				
	EARLY	<i>Turrilites costatus</i>				<i>A. primus</i>
		<i>Mantelliceras dixonii</i>			<i>A. primus</i>	
		<i>Mantelliceras saxbii</i>				
		<i>Neostlingoceras carcitanense</i>			<i>N. ultimus</i>	<i>N. ultimus</i>

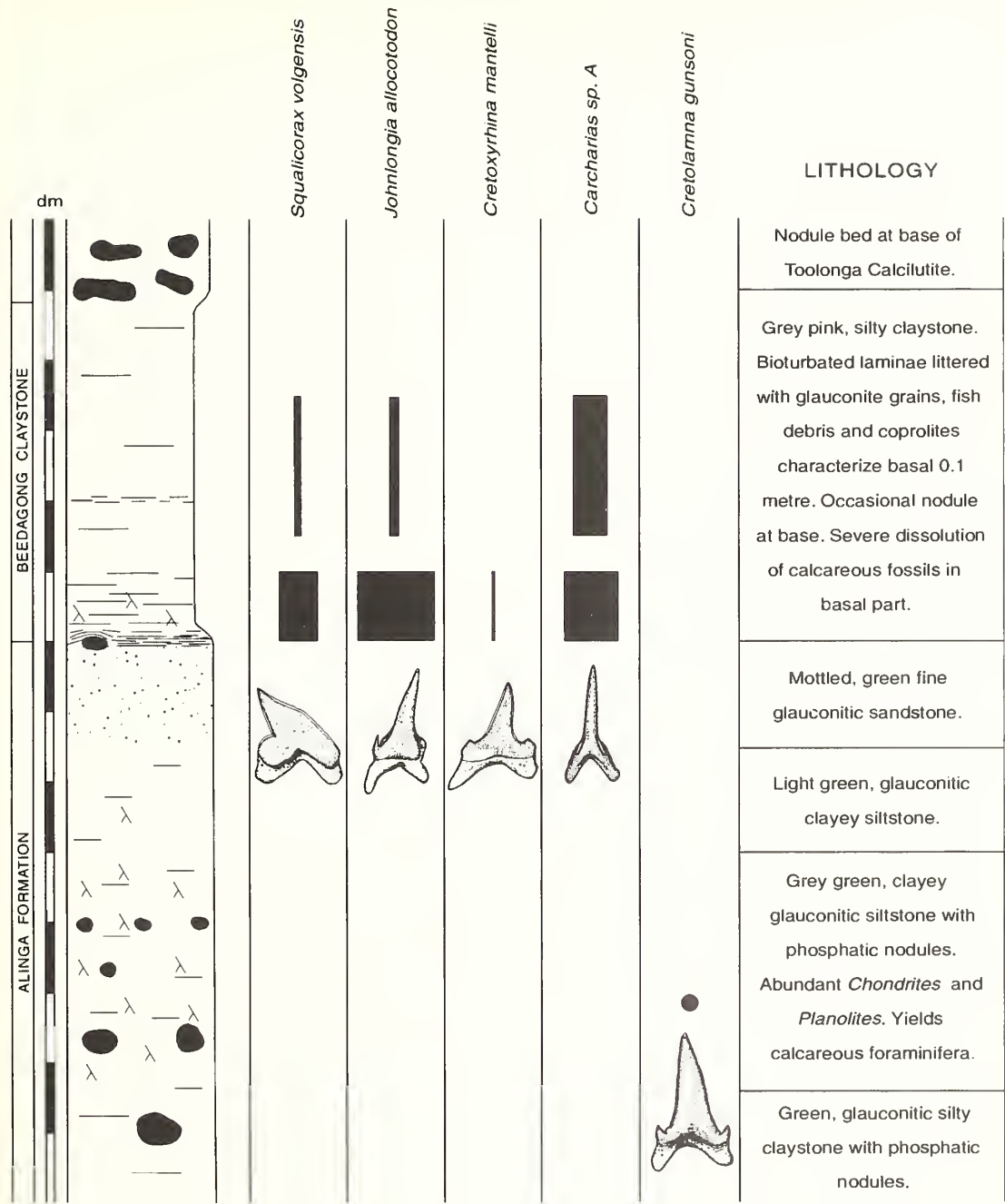
TEXT-FIG. 2. Stratigraphical diagram of the Cenomanian in northern Europe, including ammonite zones and subzones, belemnite zones, and the ranges of squalicoracid sharks and belemnites. *A.* = *Actinocamax*; *N.* = *Neohibolites*. Modified from Christensen (1993).

Beedagong Claystone. Bulk sampling (78 kg dry) of the basal 0.1 m of the Beedagong yielded teeth of four lamniform species: *Carcharias* sp. A, *Johnlongia allocotodon* gen. et sp. nov., *Squalicorax volgensis* Glikman in Glikman and Shvazhaite, 1971, and *Cretoxyrhina mantelli* (Agassiz, 1843).

Carcharias sp. A occurs elsewhere in the *Mantelliceras dixonii* and/or *Turrilites costatus* Zone/Subzone of Germany (described as *Eostriatolamia? subulata* by Müller and Diedrich 1991).

Another species of *Johnlongia* gen. nov., closely related to *J. allocotodon* gen. et sp. nov., occurs in the Turonian Carlile Shale of South Dakota and was described as *Odontaspis parvidens* by Cappetta (1973). The genus is also present in the Albion of Queensland (Noel Kemp and David Ward, pers. comm.).

Squalicorax volgensis was originally described from the *Actinocamax primus* Zone (Text-fig. 2) of the Saratov Province, Russia (Glikman and Shvazhaite 1971). It was later recorded by Müller and Diedrich (1991), as *Pseudocorax primulus*, from the *Mantelliceras dixonii* and/or the *Turrilites costatus* Zone/Subzone of Ascheloh at the Teutoburger Wald, north-west Germany. It ranges down into the late Albion; Welton and Farish (1993) described it from the Weno Formation in Tarrant County, Texas as *Squalicorax* sp. Moreover, Naidin (1981) reported it from the south-western part of the Crimean Range, Ukraine, in beds yielding *Turrilites costatus*. However, no teeth were illustrated, so this record cannot as yet be confirmed. The species has not been recorded from the younger half of the Cenomanian although descendants of it, having evolved teeth with a shorter and broader cusp, occur in the middle Turonian of the Western Interior of the United States (pers. obs.).



TEXT-FIG. 3. Section of the Beedagong Claystone and the uppermost 0.8 m of the underlying Alinga Formation at the eastern slope of the Thirindine Point ridge, showing known vertical distribution of lamniform sharks' teeth, identified at species level. Width of the bars correlates directly with the abundance of teeth in the sediment.

There is a minor difference between the late Albian *S. volgensis* teeth from Texas and the Cenomanian ones from Germany in that the basal edge of the root is more deeply notched in the latter ones. The Beedagong teeth conform perfectly in this regard with those from Germany, indicating an age closer to the late early/early mid Cenomanian than to the late Albian.

Cretoxyrhina mantelli is represented by five teeth, one from an adolescent or adult individual (Pl. 1, figs 13–14), the other four from very young ones. Lateral cusplets are developed in two of the four juvenile teeth (see e.g. Pl. 1, figs 5–6). The most conspicuous evolutionary trend in *Cretoxyrhina* Glikman, 1958 is the progressive loss of lateral cusplets, starting with the teeth of the anterior files. Biddle (1993) illustrated teeth from the middle Albian of the Saint-Dizier region, north-east France that appear to belong to the earliest known *Cretoxyrhina*. In this species, referred to *Cretoxyrhina woodwardi* (Herman, 1977) by Biddle, lateral cusplets are still present on all teeth.

Unfortunately, there is a total lack of well-dated and well-illustrated teeth of *Cretoxyrhina* from the late Albian to mid Cenomanian interval. Although Welton and Farish (1993) provided excellent documentation of an associated set of teeth from one individual from the Cenomanian part of the Britton Formation, Eagle Ford Group, in Dallas County, Texas, this reveals nothing about the intraspecific dental variation in the Britton population of *C. mantelli*. The precise stratigraphical position of the specimen within the formation was not mentioned. In the Dallas area the basal 1.5 m of the Britton Formation is of mid Cenomanian *Acanthoceras amphibolum* Zone age (Kennedy and Cobban 1990). No diagnostic macrofossils were recorded by Kennedy (1988) from the succeeding 35 m of bentonitic Britton shales, after which the mid late Cenomanian *Sciponoceras gracile* Zone fauna appears and continues to near the top of the formation (Kennedy 1988). The uppermost 2.5 m are of early Turonian age. In the Britton *C. mantelli*, minute cusplets are present on the second upper lateral tooth and on teeth of the posterior half of both the upper and lower jaw dental series.

Typical *C. mantelli* are also present in the late Cenomanian *Actinocamax plenus* Zone of Bettrechies, northern France (Herman 1977, pl. 9, fig. 6a–b) and Chercq, Belgium (Leriche 1902, pl. 3, fig. 49). The French specimens are both anterior teeth lacking cusplets, whereas the tooth figured by Leriche is a lateral one, likewise without cusplets. The species persisted into the Campanian with a youngest reliably dated occurrence (Siverson 1992) in strata in southern Sweden correlating with the latest early Campanian *Gonioteuthis quadrata gracilis*/*Belemnites mucronata* senior Zone of Schulz *et al.* (1984).

As it is, the presence of *C. mantelli* in the basal part of the Beedagong Claystone does not allow a more precise dating than can be deduced from the presence of *S. volgensis*, *Carcharias* sp. A, and *Johnlongia allocotodon* gen. et sp. nov.

A sample (80 kg dry) from the middle third of the Beedagong on the eastern slope of the Thirindine Point ridge, 0.15–0.35 m above its base, yielded the lamnoids *Carcharias* sp. A, *Johnlongia allocotodon* gen. et sp. nov. and *Squalicorax volgensis* (Text-fig. 3).

Alinga Formation. Preliminary bulk sampling from a level 0.70–0.95 m below the top of the formation has yielded fragments of squalicoracid teeth, showing well-developed serrations on the cutting edges. Comparison with complete teeth of *Squalicorax volgensis* from the basal Beedagong Claystone revealed that the Alinga fragments cannot be assigned to that species. The material is, however, taxonomically indistinguishable from some of the surface collected teeth referred herein to *Squalicorax* ex gr. *curvatus* (Williston, 1900). The earliest well-dated squalicoracids of the *S. curvatus* group with regular serrations on the cutting edges are from near the lower/middle Cenomanian boundary. Müller and Diedrich (1991) figured two serrated cusps of a large squalicoracid, possibly *S. curvatus* itself, as *S. falcatus* (Agassiz, 1843) from their *Mantelliceras dixonii* Zone/Subzone or *Turrilites costatus* Zone/Subzone fauna of the Teutoburger Wald.

Conclusions. The basal part of the Beedagong Claystone at Thirindine Point is probably of early and/or mid Cenomanian age. The presence of *Squalicorax* ex gr. *curvatus* close to a metre below the base of the Beedagong, suggests that the uppermost beds of the Alinga Formation are of post-Albian age. This part of the section is provisionally assigned to the early Cenomanian.

Alinga Point section

Preliminary bulk sampling of the upper 5 m of the Alinga Formation at Alinga Point, where the 15 m thick type section is located, showed that the Beedagong Claystone is missing here. So far, only a small number of selachian teeth has been recovered from the Alinga Point samples, none of which belongs to lamniform sharks. The faunal composition from the various sampled levels is much the same as from the uppermost metre of the Alinga Formation at Thirindine Point. This indicates that the top of the Alinga Formation at Alinga Point is not younger than early Cenomanian or possibly mid Cenomanian.

Institutional abbreviations. FHSM: Sternberg Memorial Museum, Fort Hays State University, Fort Hays, Kansas; WAM: Western Australian Museum, Perth.

SYSTEMATIC PALAEOONTOLOGY

Tooth terminology. In accordance with the recommendation by Ward (1987), the terminology used herein is after Cappetta (1987).

Order LAMNIFORMES Berg, 1958

Family CRETOXYRHINIDAE Glikman, 1958 *sensu* Cappetta, 1987

Genus CRETOXYRHINA Glikman, 1958

Type species. By original designation, *Oxyrhina mantelli* Agassiz, 1843.

Remarks. In spite of having designated *Oxyrhina mantelli* as the type species of *Cretoxyrhina* in the original description of that genus, published in 1958, Glikman (1964a) gave *Isurus denticulatus* Glikman, 1957 as the type species of *Cretoxyrhina*. An English translation of Glikman's 1964a paper was published in Jerusalem in 1967. Unfortunately, western workers relied on the misleading information in the translated, 1964 paper (e.g. Cappetta 1987; Siverson 1992).

In Glikman's figured sample of teeth from *C. denticulata* (pl. 1, figs 1–17), described from Cenomanian strata near Saratov, Russia, lateral cusplets are present in lateroposterior teeth but absent in anterior ones. In *C. mantelli*, absence or presence of cusplets on lateral and posterior teeth is largely related to the age of the material. In earlier populations, such as that from the basal Beedagong Claystone, cusplets are commonly present, whereas in later populations (Santonian–early Campanian) cusplets are usually absent, at least in lateral files.

Besides the two nominal species discussed above, Herman (1977) also referred *Lamna acuminata* Agassiz, 1838 to *Cretoxyrhina*. I strongly suspect that similarities in tooth morphology between '*L.*' *acuminata* and *Cretoxyrhina denticulata/mantelli* are due to convergent evolution. Zhelezko (1990) made '*L.*' *acuminata* the type of his new genus *Acrolamna*.

Teeth of a new, as yet unnamed *Cretoxyrhina* occur in the middle Albian of north-eastern France and were described as *Cretoxyrhina woodwardi* by Biddle (1993). This taxon is also present in the Albian of Western Australia (pers. obs).

Cretoxyrhina mantelli (Agassiz, 1843)

Plate 1, figures 1–18

- * 1843 *Oxyrhina mantelli* Agassiz, p. 280, pl. 33, figs 1–5, 7–9, non fig. 6.
- . 1975 *Cretoxyrhina mantelli* (Agassiz); Cappetta and Case, p. 20, pl. 5, fig. 27.
- . 1977 *Cretoxyrhina mantelli* (Agassiz); Herman, p. 219, pl. 9, fig. 6a–e [contains synonyms prior to 1973].
- v. 1978 *Oxyrhina mantelli*; Bergström and Sundquist, p. 11, fig. 2g.
- . 1980 *Cretoxyrhina mantelli* (Agassiz); Glikman, pl. 27, figs 13–14; pl. 29, figs 19–21.
- . 1981 *Isurus mantelli*; Witzke, p. 108, pl. 1, figs 22–28.
- v. 1983 *Oxyrhina mantelli*; Bergström, p. 101, fig. 30g.
- . 1987 *Cretoxyrhina mantelli* (Agassiz); Longbottom and Patterson, p. 250, text-fig. 11.2r, pl. 54, fig. 5.

- .1987 *Cretoxyrhina mantelli* (Agassiz); Cappetta, p. 99, fig. 87e-i.
- .1990 *Cretoxyrhina mantelli* (Agassiz); Case *et al.*, p. 1087, fig. 9a-f.
- v.1992 *Cretoxyrhina mantelli* (Agassiz); Siverson, p. 526, pl. 1, figs 18-19.
- .1993 *Cretoxyrhina mantelli* (Agassiz); Welton and Farish, p. 101, unnumbered plate; p. 102, unnumbered plate.
- .1993 *Cretoxyrhina mantelli* (Agassiz); Williamson *et al.*, p. 456, fig. 6.10-6.15.

Material. Twenty teeth from the Thirindine Point ridge; five of these are from the basal 0.1 m of the Beedagong Claystone (WAM 95.7.32, 95.7.36, 96.3.10-96.3.12) and 15 teeth (WAM 95.7.29-95.7.31, 95.7.33-95.7.35, 95.7.37, 96.3.1-96.3.8) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

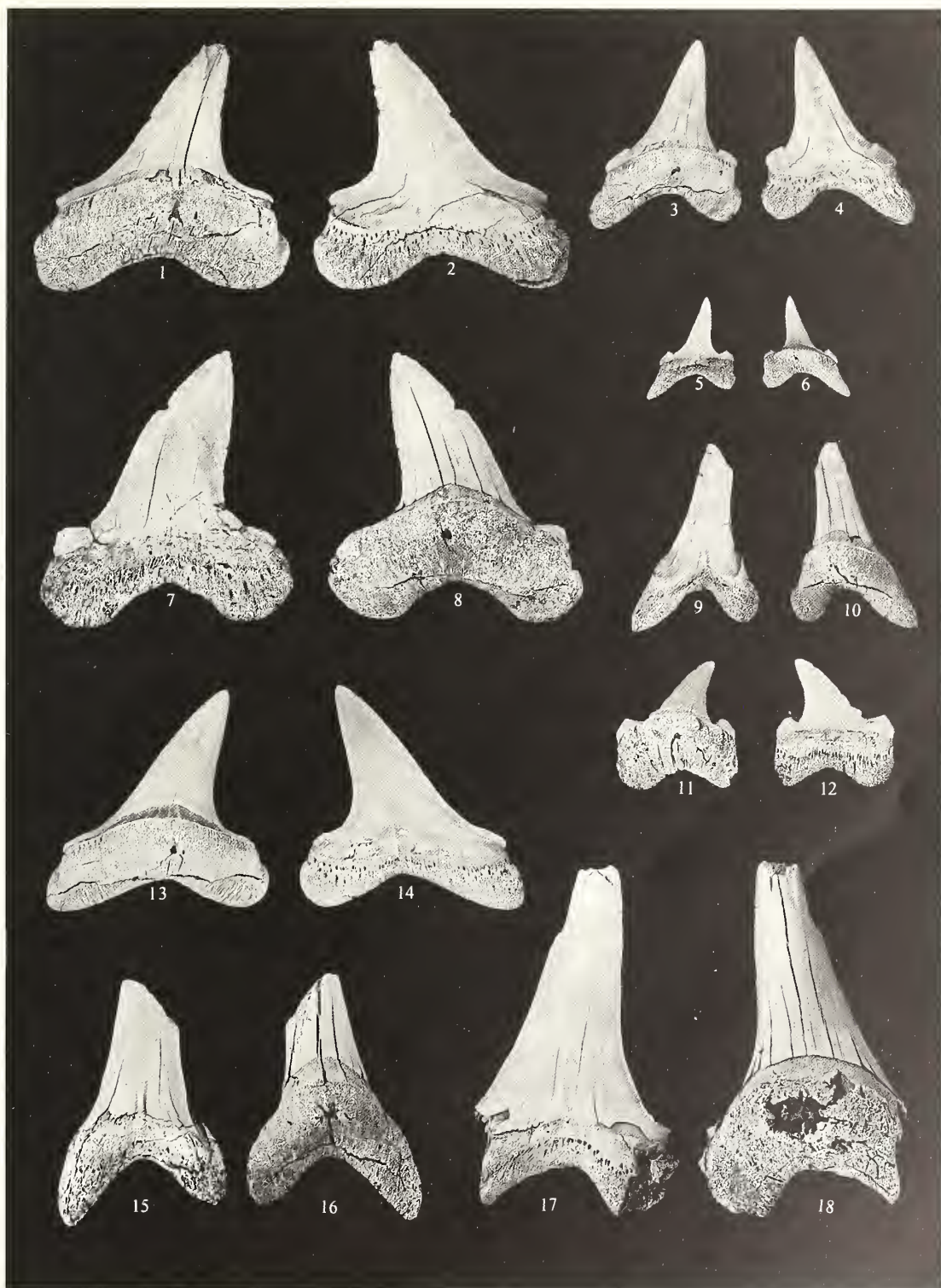
Additional occurrences. Cosmopolitan, for details see Cappetta (1987, p. 99) and also Siverson (1992) for post-Santonian occurrences.

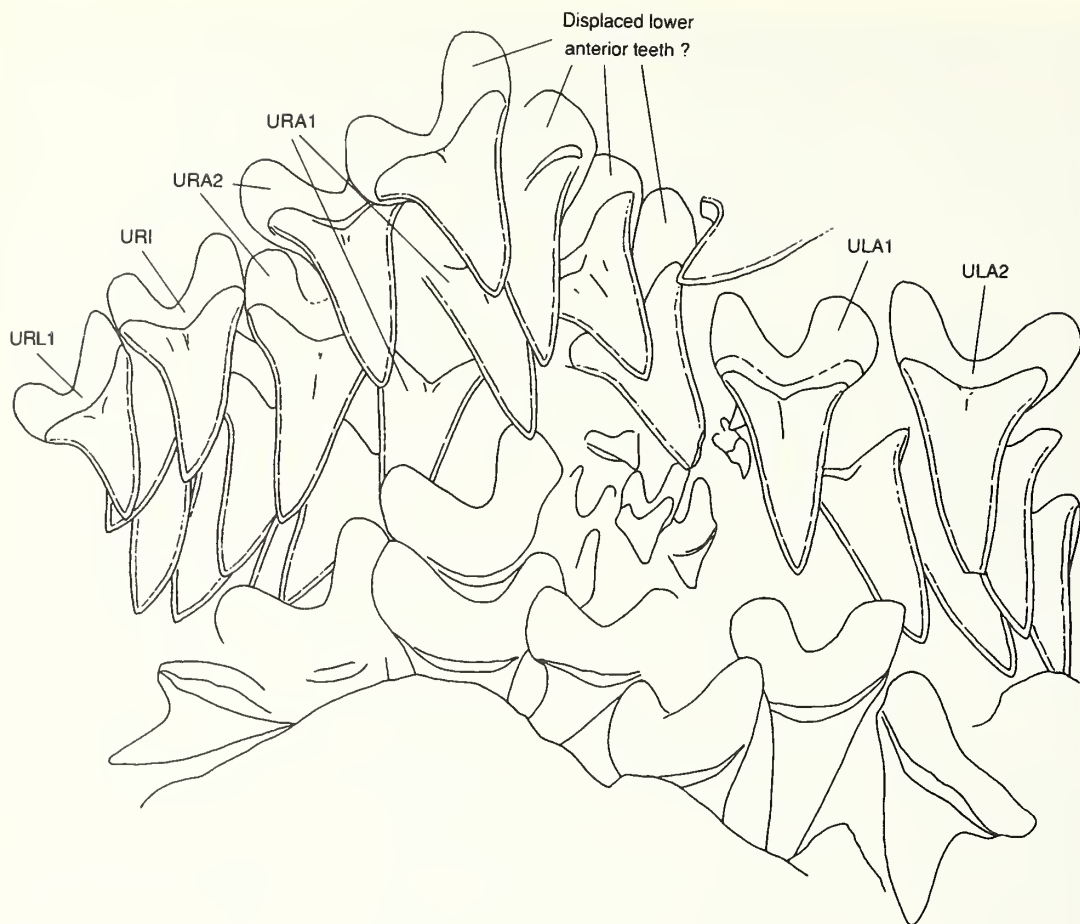
Description. In addition to the direct evidence of the arrangement of the upper jaw dental series presented here (Text-fig. 4), see also Eastman (1895) and Welton and Farish (1993) for different reconstructions of the dentition of this species based on associated but displaced teeth belonging to single individuals.

Remarks. The Western Interior Cretaceous Seaway of North America has yielded excellent material of *Cretoxyrhina mantelli*. As well as isolated teeth, the fossil remains include associated sets of teeth from single individuals (Eastman 1895; Welton and Farish 1993) together with articulated skeletons showing parts of the dentition still in place (Text-fig. 4; Siverson 1992; Shimada 1993). An associated set of displaced teeth from one individual of *C. mantelli*, collected from the mid to late Cenomanian (Kennedy 1988) part of the Britton Formation of Texas, provided Welton and Farish (1993, p. 102) with an opportunity to reconstruct the dentition. Their interpretation is in part at variance with what can be observed in the partly articulated upper dental series of a *C. mantelli* from the Smoky Hill Chalk Member of the Niobrara Formation of Kansas (FHSM VP-2187). The Niobraran specimen features two files of large, upper anterior teeth (Text-fig. 4), contrasting with the single one in Welton and Farish's reconstruction. In VP-2187 there is one file of intermediate teeth, identified as such by their distally curved cusps and almost symmetrical roots with a deeply notched basal edge. The intermediate tooth is larger than that of the first lateral file. Not appreciating this unusual condition, Siverson (1992, p. 528) considered the smallish teeth of the first lateral file to belong to a second intermediate file. The upper intermediate tooth in VP-2187 looks much like the tooth illustrated in a parasymphysial position by Welton and Farish. To the intermediate file, Welton and Farish referred a minute tooth with a morphology very similar to that of some of the upper symphysial teeth in VP-2187. The lateral teeth in VP-2187 show an initial increase in size towards the commissure followed by a decrease. This pattern is also present in some living lamnoids, such as *Isurus oxrinchus* Rafinesque, 1810 (see Bass *et al.* 1975, pl. 9).

EXPLANATION OF PLATE I

Figs 1-18. *Cretoxyrhina mantelli* (Agassiz, 1843). 1-2, WAM 95.7.30; 21.5 mm high lateral tooth, lingual and labial view; Thirindine Point west. 3-4, WAM 95.7.31; 16.5 mm high upper lateral tooth (UL2?) from a juvenile individual, lingual and labial view; Thirindine Point east. 5-6, WAM 95.7.32; 8.5 mm high upper lateral tooth (UL2?) from a very young individual, labial and lingual view; Thirindine Point east, 78 kg sample from the basal 0.1 m of the Beedagong Claystone. 7-8, WAM 95.7.33; 23.5 mm high lateral tooth, labial and lingual view; Thirindine Point west. 9-10, WAM 95.7.34; 16 mm high ?upper anterior tooth from a juvenile individual, apex of cusp broken off, labial and lingual view; Thirindine Point west. 11-12, WAM 95.7.35; 11 mm high posterior tooth, lingual and labial view; Thirindine Point east. 13-14, WAM 95.7.36; 19.5 mm high lateral tooth, lingual and labial view; Thirindine Point east, 78 kg sample from the basal 0.1 m of the Beedagong Claystone. 15-16, WAM 95.7.37; 22 mm high anterior tooth, labial and lingual view; Thirindine Point west. 17-18, WAM 95.7.29; 31 mm high anterior tooth from a large individual, apex of the cusp and both extremities of the root are broken off, labial and lingual view; Thirindine Point east. All $\times 1.8$.





TEXT-FIG. 4. Symphyseal area of the dentition of a *Cretoxyrhina mantelli* from the Niobrara Formation of Kansas (FHSM VP-2187). Note the presence of two files of anterior teeth in the upper jaw and the large size of the upper intermediate tooth. ULA1 = upper left 1st anterior; ULA2 = upper left 2nd anterior; URA1 = upper right 1st anterior; URA2 = upper right 2nd anterior; URI = upper right intermediate; URL1 = upper right 1st lateral. *Camera lucida* drawing from a photograph.

In his work on Cretaceous and Tertiary chondrichthyans of Australia, Kemp (1991) referred three of the teeth illustrated to *Cretoxyrhina*. One of them (WAM 60.90.1; Kemp 1991, pl. 4, fig. g), supposedly from the late Maastrichtian Miria Marl, Southern Carnarvon Basin, Western Australia, was figured as *Cretoxyrhina mantelli*. Examination of the imperfectly preserved tooth has revealed that it is not from a *Cretoxyrhina* but probably belonged to *Otodus obliquus* (Agassiz, 1843). The latter species is quite common in the Boongerooda Greensand of Thanetian (late Palaeocene) age which overlies the Miria Marl unconformably in the Giralia Anticline of the Southern Carnarvon Basin. The tooth is thus both misidentified and misplaced stratigraphically. The youngest reliable records of *C. mantelli* appear to be from the Kristianstad Basin, southern Sweden (Siverson 1992). There, it occurs sparsely in strata that correlate with the latest early Campanian *Goniatites quadrata gracilis*/*Belemnitella mucronata senior* Zone (*sensu* Schulz *et al.* 1984). The second tooth (WAM 62.8.29), from the late Santonian *Uintacrinus*/*Marsupites* zones of the Gingin Chalk, Molecap Hill Quarry, Perth Basin, was illustrated by Kemp (1991, pl. 4, fig. h) under the name *Cretoxyrhina cf. mantelli*. This identification is also in error. The tooth-crown

probably belongs to *Cretolamna appendiculata*. The third specimen, from the Aptian or Albian of Aramac, central Queensland, is poorly preserved and generically indeterminable. Kemp figured it as *Cretoxyrhina*? (pl. 4, fig. i).

Genus *ARCHAEOLAMNA* Siverson, 1992

Type species. *Odontaspis kopingensis* Davis, 1890, 'Köpinge sandstone' (latest early Campanian to mid late Campanian [*sensu germanico*]), Skåne, Sweden.

Remarks. Until now *Archaeolamna* was monospecific, comprising the type species *A. kopingensis* with its two geographically separated subspecies *A. k. kopingensis*, from the Campanian–Maastrichtian of the Anglo–Franco–Belgian Basin and southern Sweden, and *A. k. judithensis*, from the Campanian of the Western Interior Seaway of North America. The type species was recently also recorded under various names from the Santonian–Campanian of the Russian Platform (Zhelezko, 1990, pl. 9, figs 1–14 and pl. 10, figs 1–25). An *Archaeolamna* from the middle Albian of north-eastern France was described by Biddle (1993) as *A. kopingensis*. However, in *A. kopingensis* the lingual protuberance of the root displays a small median foramen, whereas in the Albian teeth from France the protuberance is divided by a distinct median groove. In an Albian population of *Archaeolamna* from the Gearle Siltstone in the Giralia Anticline of the Southern Carnarvon Basin, Western Australia, a median groove is present in juveniles but closed in adults (pers. obs.). Teeth of juvenile Campanian *A. kopingensis* conform with those of coeval adults in lacking a median groove. Loss of a median groove on the root protuberance took place independently in several of the Cretaceous cretoxyrhinids.

Archaeolamna aff. *kopingensis*

Plate 2, figures 1–6

Material. Four teeth from the Thirindine Point ridge; all of them (WAM 95.7.38–95.7.40, 96.3.9) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Description. In size and morphology these teeth are very close to those of mid Campanian *A. kopingensis* from southern Sweden (see Siverson 1992 for a detailed description). One of the upper lateral teeth from the Alinga Formation/Beedagong Claystone has short but strong labial folds along the base of the crown below the cusplets (WAM 95.7.40; Pl. 2, fig. 6). In *A. kopingensis*, such folds are present only in teeth from approximately the posterior quarter of the tooth row (see Siverson 1992, pl. 2, figs 8–9).

Remarks. One of the upper lateral teeth (WAM 95.7.40) of *A. aff. kopingensis* resembles one of the type specimens of *Pseudoisurus tomosus*, the latter figured in lingual view by Glikman (1957, pl. 1, fig. 20). However, the Russian specimen has a relatively broader neck and is much larger (about 30 mm high) than any upper lateral teeth of *Archaeolamna* that I have examined, including WAM 95.7.40, which is 18 mm high.

Archaeolamna haigi sp. nov.

Plate 2, figures 7–13

Derivation of name. After Dr David Haig, Department of Geology, University of Western Australia, in recognition of stimulating discussions on the Cretaceous geology of Western Australia.

Holotype. WAM 95.7.41; Plate 2, figures 7–9, upper anterior tooth; Thirindine Point Ridge (eastern slope); uppermost metre of Alinga Formation or basal part of Beedagong Claystone.

Paratypes. WAM 95.7.42 and WAM 95.7.43; Plate 2, figures 10–13.

Additional material. Nine teeth from the Thirindine Point ridge; all of them (WAM 96.3.13–96.3.21) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Diagnosis. Lingual face of crown with flexuous folds. Labial face of cusp often concave in anterior teeth. Lower laterals erect and symmetrical. Root slender and, in lateral files, labiolingually compressed.

Description. Anterior teeth are up to 20.5 mm high. There is one pair of triangular cusplets. The labial face of the cusp is slightly convex to concave and smooth; the lingual face is much more cambered and, together with the cusplets, with weak to moderately well-marked flexuous folds. The lingual face of the cusp is medially flattened in some anterior teeth, giving the cusp a sub-rectangular cross section. Lower lateral teeth are erect, have one pair of triangular cusplets and feature prominent lingual folds. The lingual protuberance of the gracile root features an apicobasally elongated median foramen.

Comparison. The teeth of *A. haigi* sp. nov. are easily separated from those of the only other valid named species of the genus, *A. kopingensis*, by their lingual folds on the crown and significantly more slender root. Moreover, lower lateral teeth are always asymmetrical in *A. kopingensis* with a cusp slightly bent towards the commissure, whereas in *A. haigi* sp. nov. the lower lateral teeth are symmetrical. In most of the anterior teeth of *A. haigi* sp. nov., the labial face of the cusp is concave. In *A. kopingensis* the labial face is slightly convex, never concave.

Remarks. With dental features like flexuous lingual folds, bilateral symmetry and a labiolingually compressed root in lower lateral files, and slender anterior teeth, *A. haigi* had convergently acquired a tooth morphology approaching that of some odontaspids like *Carcharias*.

Genus LEPTOSTYRAX Williston, 1900

Type species. *Leptostyrax bicuspidatus* Williston, 1900, from the Albian Mentor Beds of Kansas, USA.

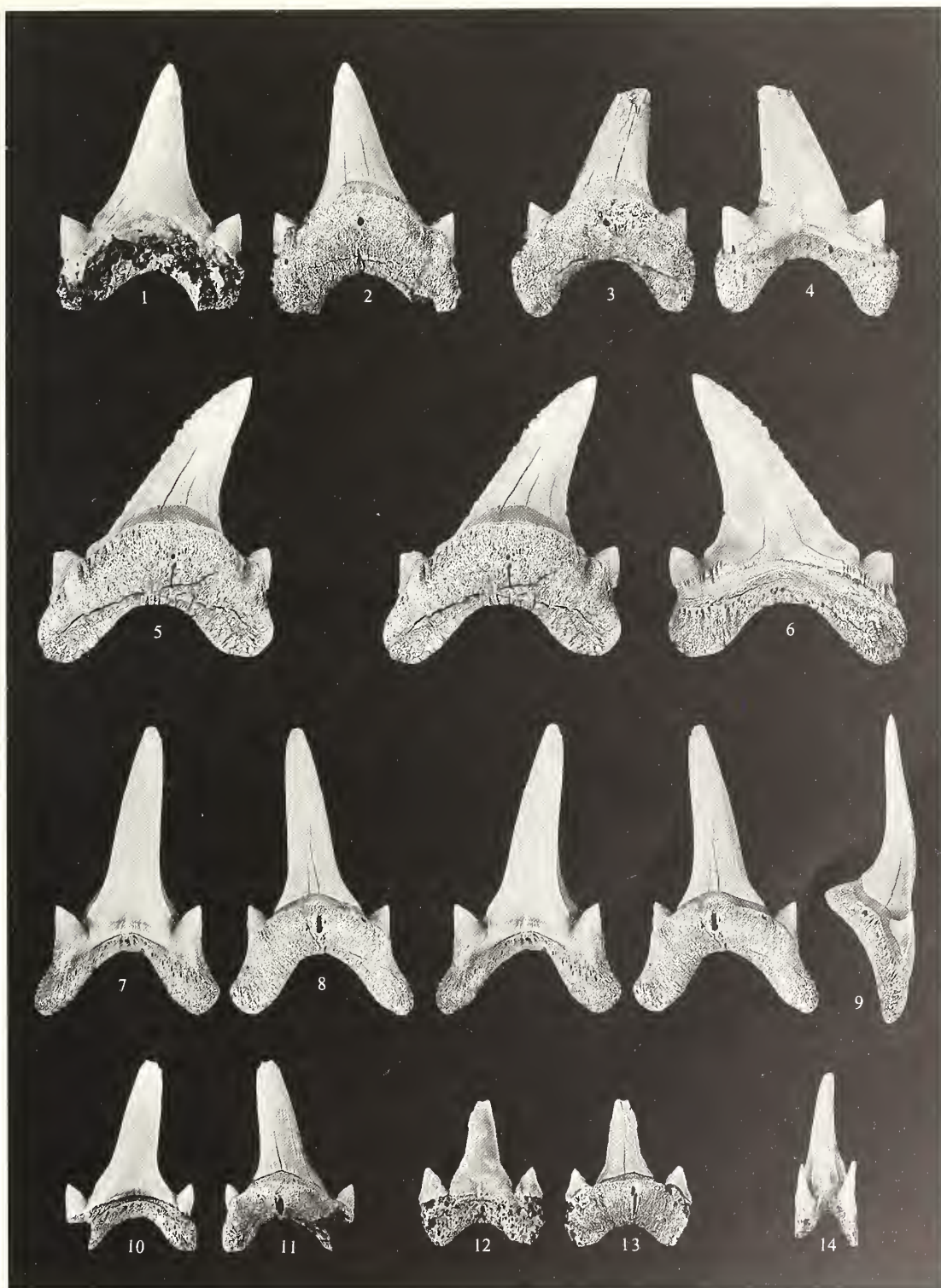
Remarks. Cappetta (1987) and Siverson (1992) referred *Leptostyrax* to the family Cretoxyrhinidae. This view was apparently not shared by Biddle (1993), who argued that there are important differences in the dental series between *Leptostyrax* and true cretoxyrhinids. According to Biddle, cretoxyrhinids possess no parasymphysial teeth and only a single upper intermediate file, whereas in *Leptostyrax* there is a parasymphysial file as well as multiple files of intermediate teeth. A *Cretoxyrhina mantelli* specimen (FHSM VP-2187) from the Niobrara Formation of Kansas includes parts of the upper jaw dentition still in place, showing the presence of dwarfed parasymphysial teeth (Text-fig. 4). Thus, application of Biddle's definition of Cretoxyrhinidae would exclude *Cretoxyrhina*

EXPLANATION OF PLATE 2

Figs 1–6. *Archaeolamna* aff. *kopingensis* (Davis, 1890). 1–2, WAM 95.7.38; 16.5 mm high lower lateral tooth, root incomplete, labial and lingual view; Thirindine Point west. 3–4, WAM 95.7.39; 15 mm high upper lateral tooth, tip of cusp missing, lingual and labial view; Thirindine Point east. 5–6, WAM 95.7.40; 18 mm high upper lateral tooth, lingual (stereo pair) and labial view; Thirindine Point east. All $\times 2.4$.

Figs 7–13. *Archaeolamna haigi* sp. nov. 7–9, WAM 95.7.41, holotype; 18.5 mm high upper anterior tooth, labial (stereo pair), lingual (stereo pair) and profile view; Thirindine Point east. 10–11, WAM 95.7.42, paratype, 12.5 mm high upper ?anterior tooth, labial and lingual view; Thirindine Point east. 12–13, WAM 95.7.43, paratype; 9.5 mm high lower lateral tooth, root incomplete, labial and lingual view; Thirindine Point east. All $\times 2.4$.

Fig. 14. *Leptostyrax* sp.; WAM 95.7.44; 9 mm high anterior tooth, root poorly preserved, labial view; Thirindine Point east; $\times 3$.



SIVERSON, *Archaeolamna*, *Leptostyrax*

mantelli from the family. Biddle's interpretation of the dentition in the designated (Cappetta 1980) type species of *Leptostyrax* was at least in part influenced by Sokolov's (1978) reconstruction of the dental series of a species from the Vraconian of the Mangyshlak Province, Kazakhstan, referred by him to *Megarhizodon macrorhiza* (Cope, 1875). Cappetta (1987) showed that *Megarhizodon* Sokolov, 1978 is a junior synonym of *Leptostyrax*. According to Cappetta (1987) the sample figured by Sokolov is not from a *Leptostyrax* but belongs to a species of *Protolamna* Cappetta, 1980. Biddle (1993) was of the opinion that the latter nominal genus is synonymous with the older *Leptostyrax*. While applying Cappetta's definition of *Protolamna* and *Leptostyrax*, Welton and Farish (1993) had no difficulty separating the two genera in a late Albian fauna from the Weno Formation of Texas.

Leptostyrax sp.

Plate 2, figure 14

Material. One tooth (WAM 95.7.44) from the Thirindine Point ridge, surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Description. An 8.9 mm high imperfectly preserved tooth. The labial face of the cusp is almost flat with the cutting edges so close together that the marginal parts of the strongly cambered lingual side can be seen in labial view. The lateral cusplets, parallel to the cusp, rise from bases below that of the cusp and are separated from it by narrow grooves. In profile view, their labial faces are in front of that of the cusp. Flexuous folds, present on both sides of the cusp and cusplets, are a little stronger and extend higher up on the labial face. The neck, separating the lingual face of the crown from the root, is about 0.6 mm wide.

The root is poorly preserved, having sustained corrosion. The lingual protuberance is mesiodistally narrow, very high and lacks a median groove.

Remarks. The small size of the tooth, compared with that of other illustrated examples of the genus, indicates that it may be from a juvenile individual. The tooth differs from those of the designated type species, *L. macrorhiza* (Cope, 1875) from the Albian of Kansas and Texas, by its mesiodistally narrower lingual protuberance of the root and relatively longer folds. The latter difference could, however, be largely or wholly due to the small size of the tooth. In *Leptostyrax* the folds are relatively shorter in larger teeth.

Genus CRETOLAMNA Glikman, 1958

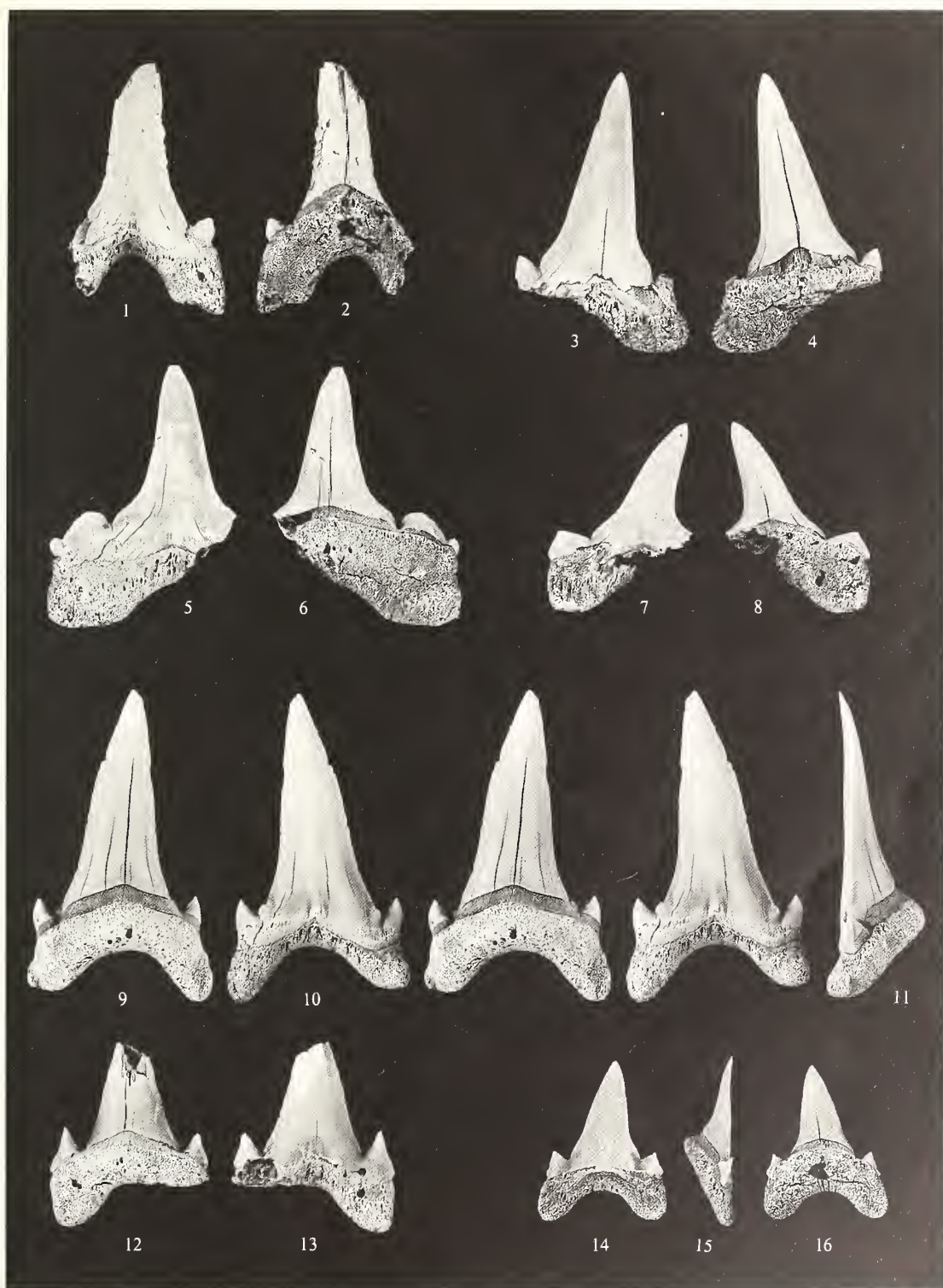
Type species. *Otodus appendiculatus* Agassiz, 1843, from the Turonian of Lewes, England.

EXPLANATION OF PLATE 3

Figs 1–8. *Cretolamna appendiculata* (Agassiz, 1843). 1–2, WAM 95.7.45; 16 mm high lower anterior tooth, tip of cusp and mesial extremity of root broken off, labial and lingual view; Thirindine Point east. 3–4, WAM 95.7.46; 18 mm high upper anterior tooth (UA2), distal cusplet and mesial portion of the root missing, labial and lingual view; Thirindine Point east. 5–6, WAM 95.7.47; 16.5 mm high lower lateral tooth, cusplet and root lobe broken off on one side, labial and lingual view; Thirindine Point east. 7–8, WAM 95.7.48; 12.5 mm high upper lateral tooth, distal lobe of root and distal cusplet missing, labial and lingual view; Thirindine Point east. All $\times 2.4$.

Figs 9–13. *Cretolamna gunsoni* sp. nov. 9–11, WAM 95.7.49; holotype; 24 mm high upper left anterior tooth (UA2), lingual (stereo pair), labial (stereo pair) and profile view; Thirindine Point east, *in situ* 0.52 m below the base of the Beedagong Claystone. 12–13, WAM 95.7.50; paratype; 14 mm high lower lateral tooth, apex of cusp and one root lobe broken off, lingual and labial view; Thirindine Point south. Both $\times 2$.

Figs 14–16. *Pseudoisurus tomosus* Glikman, 1957, WAM 95.7.51; 13.5 mm high lower lateral tooth, labial, profile and lingual view; Thirindine Point east; $\times 1.8$.



Cretolamna appendiculata (Agassiz, 1843)

Plate 3, figures 1–8

- *1843 *Otodus appendiculatus* Agassiz, p. 270, pl. 32, figs 2–8, 10–14, 16, 19, 22, 24–25, ?figs 20, 23, *non* figs 1, 9, 15, 17–18, 21.
- .1977 *Cretolamna appendiculata* (Agassiz); Herman, p. 210, pl. 9, figs 2–4 [contains synonyms prior to 1973].
- .1987 *Cretolamna appendiculata* (Agassiz); Longbottom and Patterson, p. 249, text-fig. 11.2z, pl. 54, fig. 4.
- v.1991 *Cretolamna appendiculata* (Agassiz); Kemp, pl. 4, fig. d.
- v.1991 *Cretoxyrhina* cf. *mantelli* (Agassiz); Kemp, pl. 4, fig. h.
- .1991 *Cretolamna appendiculata* (Agassiz); Müller and Diedrich, p. 31, pl. 21, figs 7–8.
- .1991 *Cretolamna appendiculata*; Landemaine, p. 13, fig. 4a.
- v.1992 *Cretolamna appendiculata* (Agassiz); Siverson, p. 528, pl. 1, figs 1–17 [contains synonyms from 1975 to 1989].
- .1992 *Otodus appendiculatus* Agassiz; Manning and Dockery III, p. 26, pl. 4, figs 5–6.
- .1993 *Cretolamna appendiculata* (Agassiz); Welton and Farish, p. 103, unnumbered plate, figs 1–5; p. 104, unnumbered plate, figs 1–2.
- .1993 *Cretolamna woodwardi* (Herman); Welton and Farish, p. 105, unnumbered plate, figs 1–3.
- .1993 *Cretolamna appendiculata* (Agassiz); Williamson *et al.*, p. 454, fig. 6.1–6.6.

Material. Five teeth from the Thirindine Point ridge; all of them (WAM 95.7.45–95.7.48, 96.3.22) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Additional occurrences. Cosmopolitan; for details see Herman (1977, p. 215).

Description. See Welton and Farish (1993) for illustration of a reconstructed tooth set of the species.

Remarks. Welton and Farish (1993, p. 104) constructed a composite tooth set of *C. appendiculata*, based on well-preserved teeth from the late Albian Weno Formation of Texas. In their reconstruction, there are two files of upper anterior teeth. As in *C. gunsoni* sp. nov., described below, I believe that there were in fact three upper anterior files in *C. appendiculata*. The two upper anterior teeth in Welton and Farish's tooth set are probably from the first and third anterior files respectively. Welton and Farish referred a dwarfed tooth to the upper jaw intermediate file. Similar teeth from the lower Campanian of the Kristianstad Basin, southern Sweden, were interpreted by Siverson (1992, pl. 1, figs 12–17) as parasymphysial teeth of the same species. Although this interpretation may be incorrect, similar teeth are indeed located at the symphysis in another cretoxyrhinid, *Cretoxyrhina nantelli* (Text-fig. 4; Siverson, 1992, p. 528).

Kemp (1991, pl. 4, figs a–e) figured five teeth from the Australian Cretaceous as *C. appendiculata*, one from the early Late Cretaceous Molecap Greensand of the Perth Basin, Western Australia (fig. d; WAM 63.9.25) and four from the Albian of the Eromanga Basin, Queensland. The Western Australian tooth is unquestionably from *C. appendiculata*. The tooth in Kemp's figure e can also be assigned with confidence to *Cretolamna* but probably not *C. appendiculata*. Very similar teeth have recently been collected from Albian strata of the Gearle Siltstone in the Giralia Anticline of the Southern Carnarvon Basin, Western Australia. They may represent a new species of *Cretolamna* and are the oldest examples of the genus. Of the remaining three teeth figured by Kemp, two (figs a–b) are definitely not *C. appendiculata*. In size and general morphology, they most closely resemble the teeth of *Pseudoisurus* Glikman, 1957 and primitive *Cretoxyrhina*. The last tooth (fig. c) is too poorly preserved to comment upon. In addition to these five specimens assigned by Kemp to *C. appendiculata*, he also illustrated a tooth under the name *Cretolamna* cf. *appendiculata* (pl. 4, fig. f). The age of this Queensland specimen is not known and it does not look like the teeth of *C. appendiculata*. Finally, as suggested above, the late Santonian tooth-crown from the Gingin Chalk of the Perth Basin, referred by Kemp to *Cretoxyrhina* cf. *mantelli* (pl. 4, fig. h) probably does represent *C. appendiculata*.

Cretolamna gunsoni sp. nov.

Plate 3, figures 9–13

Derivation of name. After Mark Gunson, Department of Geology, University of Western Australia, in recognition of field assistance.

Holotype. WAM 95.7.49; Plate 3, figures 9–11, second upper left anterior tooth; eastern slope of the Thirindine Point ridge; middle of a 0.35 m thick bed characterized by conspicuous *Chondrites* and *Planolites*, 0.52 m below the base of the Beedagong Claystone (see Text-fig. 3).

Paratype. WAM 95.7.50; Plate 3, figures 12–13, lower lateral tooth.

Additional material. Five teeth from the Thirindine Point ridge; all of them (WAM 96.3.23–96.3.27) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Diagnosis. Upper anterior teeth with gracile root, moderately labiolingually compressed. Tip of cusp curved outwards. Cusplets, narrow in juveniles, with straight to convex outer margin. Base of crown may overhang root labially.

Upper laterals with cambered labial face of distally directed cusp almost as convex as lingual face. In anteriorly situated lateral teeth, cusplets erect, higher than broad and with straight to convex outer margins. In middle part of tooth-row, cusplets usually asymmetrical with outer margin much longer than inner one. Root labiolingually compressed with angular extremities.

Lower laterals erect with cusplets higher than broad. Labial face of cusp less convex than in upper lateral teeth. Root labiolingually compressed and relatively slender.

Description. Upper anterior teeth, of which there are probably three on each side of the symphysis, reach at least 24 mm high in the Alinga Formation population. There is one pair of comparatively small cusplets which are higher than wide. The tip of the cusp is curved outwards on all upper anterior teeth. In teeth of the first upper anterior file the cusp is symmetrical. In the second upper anterior file (Pl. 3, figs 9–11), the cusp is slightly curved towards the commissure. The third upper anterior tooth features a cusp with its basal half bent somewhat distally whereas the apical half is slightly mesially curved, much as in the third upper anterior tooth of the extant *Carcharias taurus* Rafinesque, 1810. Labially, the base of the crown may overhang the root, which is rather gracile and moderately labiolingually compressed. A single circular foramen opens on a relatively high lingual protuberance.

Mesially situated upper lateral teeth have a high, distinctly distally bent cusp. The labial face of the cusp is cambered and the cusplets are erect, higher than broad and with straight inner and convex outer edges. The root is gracile and labiolingually compressed. In more posteriorly situated lateral teeth, the cusp is lower and the cusplets are distinctly asymmetrical with the outer margin significantly longer than the inner one.

Lower lateral teeth possess a more-or-less erect cusp with a relatively flat labial face. The root is labiolingually compressed and slender.

Comparisons. The teeth of *Cretolamna gunsoni* are readily separable from those of coeval *C. appendiculata* by the following features: (1) the root is markedly labiolingually compressed in the upper anterior teeth of *C. appendiculata*, less so in those of *C. gunsoni*; (2) cusplets are usually broader than high in *C. appendiculata* whereas the reverse condition prevails in *C. gunsoni*, at least in the anterior half of the dentition; (3) in upper anterior files of *C. gunsoni* the cusplets have a straight to convex outer cutting edge and are often curved toward the cusp, whereas in the corresponding teeth of *C. appendiculata* the outer edge of the cusplets is straight to concave and the cusplets are curved away from the cusp; (4) the labial face of the cusp is flat in upper lateral teeth of *C. appendiculata*, markedly convex in *C. gunsoni*; (5) in upper lateral files near the centre of the tooth row of *C. gunsoni* the outer margins of the cusplets are significantly longer than the inner ones, whereas in *C. appendiculata* they are roughly the same length; (6) in young *C. gunsoni* the cusplets

are narrow and elongated in anterior files, in contrast to juvenile *C. appendiculata* which display cusplets with a wide base on their anterior teeth.

Remarks. Teeth of *Cretolamna gunsoni* sp. nov. are common in the transitional beds between the Gearle Siltstone and the overlying Beedagong Claystone at C-Y Creek in the Giralia Anticline of the Southern Carnarvon Basin (pers. obs.).

This is the second known mid Cretaceous species of *Cretolamna*. As shown below, Herman's (1977) nominal *Cretolamna woodwardi* has a tooth morphology quite different from that of true *Cretolamna* and is here regarded as a junior synonym of *Pseudoisurus tomosus*.

Genus PSEUDOISURUS Glikman, 1957

Type species. *Pseudoisurus tomosus* Glikman, 1957, from the upper Cenomanian (in the Russian two-fold division of the stage) of the Volga area, Russia.

Remarks. Siverson (1992) shared the views of Herman (1977) and Cappetta (1987) that *Pseudoisurus* is a poorly defined genus and indicated that it might prove to be synonymous with *Archaeolamna* Siverson, 1992. New material from the Albian and Cenomanian of Western Australia indicates that both nominal genera are valid. Glikman's (1957) original description of *Pseudoisurus tomosus* is accompanied by illustrations of four teeth (pl. 1, figs 17–20). One of them is rather poorly preserved (fig. 18) and another is figured in profile view only (fig. 19), limiting their usefulness for comparisons. The remaining two teeth (figs 17, 20) are both from upper lateral tooth-files. They are almost perfectly matched by two corresponding teeth from the Thirindine Point ridge (Pl. 4, figs 3–4, 8–10). However, the latter two teeth are probably specifically, if not generically, distinct from each other. Both are imperfectly preserved, lacking their distal cusplet and parts of the distal lobe of the root. The larger tooth (WAM 95.7.28; Pl. 4, figs 8–10), very similar to the tooth in Glikman's figure 20, is markedly curved toward the rear. The labial face of the cusp is distinctly convex and the mesial and distal cutting edges of the mesial cusplet are equal in length. Moreover, in occlusal view the apical half of the cusp is slightly rotated anti-clockwise. The smaller tooth (WAM 95.7.53; Pl. 4, figs 3–4), closely resembling the tooth in Glikman's figure 17, features a cusp moderately bent toward the commissure. The labial face of the cusp is flat and the mesial cutting edge of the mesial cusplet is almost twice as long as the distal edge. Six additional teeth in the collection from the transitional beds between the Alinga Formation and the Beedagong Claystone conform closely to WAM 95.7.53 with regard to the very flat labial face of the cusp and shape of the lateral cusplets. These seven latter teeth grouped together appear specifically inseparable from two sets of associated teeth from the middle or upper Cenomanian of southern England, figured as *Lamna appendiculata* (Agassiz, 1843) by Woodward (1894). The latter taxon is the type species of *Cretolamna* Glikman, 1958. Herman (1977) rightly considered the English teeth to be distinct from those of *C. appendiculata* and proposed the new nominal species *Cretolamna woodwardi* to accommodate them.

As can be gathered from the discussion above, the Western Australian material indicates that the Cenomanian nominal species *Cretolamna woodwardi* and *Pseudoisurus tomosus* are at least in part synonymous and that the latter may be based on a mixture of two different taxa. For the time being I treat Glikman's figured sample of *P. tomosus* as homogeneous and wholly conspecific with Herman's *C. woodwardi*. The former nominal species takes priority by 20 years. I do not agree with Herman's generic assignment of the species, in particular the morphology of the root in upper lateral teeth is very different in true *Cretolamna* and *P. tomosus* (= *C. woodwardi*).

Dental differences between *Pseudoisurus*, as defined herein, and *Archaeolamna* include: (1) in upper lateral files the cusp usually expands more or less abruptly in width within the basal third of its height in *Archaeolamna* (see e.g. Woodward 1894, pl. 6, fig. 10; Herman 1977, pl. 8, fig. 4i; Siverson 1992, pl. 2, fig. 12; Pl. 2, fig. 6), whereas in adult *Pseudoisurus* the cusp increases more linearly in width toward its base (Woodward 1894, pl. 5, fig. 25; pl. 6, fig. 2); (2) the lingual neck is medially very wide in anterior teeth of *Pseudoisurus* (Woodward 1894, pl. 6, fig. 2f); less so in

Archaeolamna (Herman 1977, pl. 8, fig. 4d, g; Case 1987, pl. 3, fig. 8); (3) the inner and outer cutting edges of the cusplets are of equal length in *Archaeolamna* whereas in *Pseudoisurus* the outer one is often significantly longer than the inner one, especially on the mesial cusplet (Pl. 4, fig. 1); (4) the dental ontogeny in the two genera differs in that the shape of the lateral cusplets does not change markedly during ontogeny in *P. tomosus*, whereas in *Archaeolamna* the cusplets are high and slender in juveniles but relatively lower and with a broader base in adults.

It should also be pointed out that the teeth of *P. tomosus* reach a considerably larger maximum size (about 40 mm in height) than those of coeval *Archaeolamna* (about 25 mm in height).

Pseudoisurus tomosus Glikman, 1957

Plate 3, figures 14–16; Plate 4, figures 1–4

- 1894 *Lamna appendiculata* (Agassiz); Woodward, p. 197, pl. 5, fig. 25, pl. 6, fig. 2.
- 1912 *Lamna appendiculata* (Agassiz); Woodward, p. 206, text-figs 63–64; pl. 44, figs 6, ?.
- * 1957 *Pseudoisurus tomosus* Glikman, p. 116, pl. 1, figs 17–20.
- 1964a *Pseudoisurus tomosus* Glikman; Glikman, p. 230, pl. 4, fig. 6.
- ?1977 *Cretolamna woodwardi* Herman, p. 207, pl. 9, fig. 1a–b.
- 1980 *Pseudoisurus tomosus* Glikman; Glikman, pl. 17, fig. 14.

Material. Seven teeth from the Thirindine Point ridge; all of them (WAM 95.7.51–95.7.53, 96.3.28–96.3.31) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Additional occurrences. Upper Cenomanian (in the Russian two-fold division of the stage) of the Saratov region, Russian Platform; middle or upper Cenomanian of Maidstone and Dover, southern England; and possibly the upper Cenomanian (*Actinocamax plenus* Zone) of Bettrechies, northern France and the Turonian (*Terebratulina rigida* Zone) of Chercq, Belgium.

Emended diagnosis. Anterior teeth erect with tall, narrow to moderately broad cusp. Lower laterals almost symmetrical; upper ones with distally directed cusp. Crown smooth, at least in anterior and lateral teeth. Labial face of cusp very flat. Cutting edges continuous, without serrations. One pair of broad-based lateral cusplets. Mesial cusplet with outer margin about one-and-a-half times to twice as long as the inner one. Root thick and of similar appearance in all files with basal edge forming open, evenly curved arch. Lingual protuberance without median grooves. Lobes well separated and diverging with rounded extremities. Lingual neck wide at centre of cusp in anterior teeth but diminishes rapidly in width toward lateral margins of crown. Relative size and shape of lateral cusplets remain constant throughout ontogeny.

Description. The three selected teeth described below are the best preserved from the Thirindine Point ridge.

WAM 95.7.51 (Pl. 3, figs 14–16); a 13.5 mm high well preserved lower lateral tooth from a juvenile individual. Outer margins of the cusplets are almost twice as long as the inner ones. The basal edge of the root forms a broadly rounded open arch. Maximum labiolingual thickness of the root is about 4.1 mm.

WAM 95.7.52 (Pl. 4, figs 1–2); a 21 mm high tooth, probably from the third anterior file in the lower jaw. The specimen compares well in size and proportions with a tooth from the type series of *C. woodwardi* (see Woodward, 1894, pl. 5, fig. 25n).

WAM 95.7.53 (Pl. 4, figs 3–4); a 16 mm high upper lateral tooth from a young individual. The distal cusplet and the tip of the distal lobe of the root are missing. The mesial cusplet shows typical features of the species with an outer margin much longer than the inner one. This tooth is close in morphology to one of the type specimens of *P. tomosus* (see Glikman, 1957, pl. 1, fig. 17).

Remarks. The type material of the nominal *Cretolamna woodwardi* is Cenomanian in age. Herman (1977), Williamson *et al.* (1993) and Welton and Farish (1993) also reported it from the Turonian.

Herman's example is a well-preserved anterior tooth from Belgium. It does indeed display features typical for anterior teeth in *C. woodwardi*, including a medially well-developed neck and a

markedly concave base of the labial enameloid. However, at present, I cannot assign it to the nominal *C. woodwardi* with confidence, as it may belong to the poorly known *Pseudoisurus?* sp., described below.

The early Turonian tooth from Arizona, figured as *C. woodwardi* by Williamson *et al.* (1993, fig. 6.7–6.8) belonged to a lateral file, probably in the upper jaw. This specimen exhibits some typical traits of *C. woodwardi*, such as a well-developed neck and root lobes wide apart with the basal edge of the root forming a broad, evenly curved open arch. Nevertheless, it differs from lateral teeth of Cenomanian *C. woodwardi* by its distinctly convex rather than flat labial face of the cusp and thicker cusp in profile view. It is closer in morphology to *Pseudoisurus?* sp., described below.

Welton and Farish (1993, p. 105) figured as *C. woodwardi* three teeth from the late mid to early late Turonian (Kennedy, 1988) Arcadia Park Formation of Texas. Two of them are from anterior files whereas the third is an upper lateral tooth. The two authors were of the opinion that their material is very close in morphology to Herman's (1977) figured examples of *C. woodwardi*. It is not absolutely clear whether Welton and Farish's reference to Herman's figured material meant the English type specimens of *C. woodwardi* or the two isolated teeth from, respectively, Belgium and northern France, also referred to the species by Herman. Welton and Farish also suggested that *C. woodwardi* may be a junior synonym of *Cretolamna appendiculata*, being based on teeth from old individuals of the latter. In this view, the type specimens of *C. woodwardi* are from an old individual and the three smaller teeth from Texas figured by them as *C. woodwardi* are likewise from old sharks of the same nominal species which actually may be denominating old individuals of *C. appendiculata*. As shown herein, the uppermost beds of the Alinga Formation and/or the basal Beedagong Claystone have yielded teeth taxonomically inseparable from the type specimens of *C. woodwardi*. The collection includes teeth from juveniles as well as older individuals. The juvenile specimens are as distinct from the teeth of *C. appendiculata* as are those from old individuals. Consequently, Welton and Farish's hypothesis that *C. woodwardi* possibly denominates teeth from old individuals of *C. appendiculata* is rejected. In the description of their material referred to *C. woodwardi*, Welton and Farish pointed out that the lateral teeth are very close in morphology to those of *C. appendiculata*. It seems likely that the upper lateral tooth figured by them as *C. woodwardi* resembles the corresponding ones of *C. appendiculata* simply because it is indeed a tooth from the latter species. From Woodward's illustrations of the two English sets of associated teeth, one of which comprises the type series of *C. woodwardi*, it is obvious that the root in upper lateral teeth of that species is different from the characteristic, angular one in *C. appendiculata*. The two anterior teeth figured by Welton and Farish are superficially similar to the Turonian tooth from Belgium figured by Herman as *C. woodwardi*, which, as indicated above, may not be from a *C. woodwardi*. Nevertheless, a closer examination reveals important differences. In the Belgian specimen, the neck is medially very well developed and in labial view the enameloid reaches

EXPLANATION OF PLATE 4

- Figs 1–4. *Pseudoisurus tomosus* Glikman, 1957. 1–2, WAM 95.7.52; 21 mm high lower anterior tooth (LA3), labial (stereo pair) and lingual view; Thirindine Point east. 3–4, WAM 95.7.53; 16 mm high upper lateral tooth (UL1 or UL2), specimen corroded and lacks distal cusplet, lingual and labial view; Thirindine Point east. Both $\times 1.8$.
- Figs 5–10. *Pseudoisurus?* sp. 5–7 WAM 95.7.27; 29.5 mm high lower lateral tooth, one cusplet missing, labial, profile and lingual view; Thirindine Point west. 8–10, WAM 95.7.28; 21.5 mm high upper lateral tooth, distal root lobe and cusplet broken off, labial (stereo pair), lingual (stereo pair) and profile view; Thirindine Point west. Both $\times 1.8$.
- Figs 11–14. *Paranomotodon* sp. 11–12, WAM 95.7.54; 14 mm high anterior tooth, lingual and labial view; Thirindine Point east. 13–14, WAM 95.7.55; 14 mm high anterior tooth, labial and lingual view; Thirindine Point east. Both $\times 2.4$.
- Figs 15–16. '*Anomotodon*' sp.; WAM 95.7.56; 16 mm high upper left anterior tooth (UA3), distal half of the root missing, lingual and labial view; Thirindine Point east; $\times 2.4$.



SIVERSON, *Pseudoisurus*, *Paranomotodon*, 'Anomotodon'

downward beyond the base of the cusplets, giving the base of the crown a markedly acute, concave outline. In contrast, the neck is only moderately developed in the two Texan teeth which are considerably smaller (assuming the scale bar is accurately drawn), and the enameloid does not extend much beyond the base of the cusplets. All three Texan teeth fall well within the range of late Cenomanian/Turonian *C. appendiculata* (see Herman, 1977, pl. 9, fig. 2). Finally, as demonstrated above, the nominal *Cretolamna woodwardi* is probably in part or wholly synonymous with the nominal *Pseudoisurus tomosus*.

Pseudoisurus? sp.

Plate 4, figures 5–10

?1977 *Cretolamna woodwardi* Herman, p. 207, pl. 9, fig. 1a–b.

?1992 *Pseudoisurus tomosus* (Glikman); Siverson, p. 530.

?1993 *Cretolamna woodwardi* Herman; Williamson *et al.*, p. 456, fig. 6.7–6.9.

Material. Two teeth from the Thirindine Point ridge; both (WAM 95.7.27–95.7.28) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Additional occurrences. The same or a closely related species occurs in the Turonian of the Western Interior (Montana, Arizona) of the USA, and possibly in the Turonian of Belgium.

Description. WAM 95.7.27 (Pl. 4, figs 5–7); a 29.5 mm high lower lateral tooth, lacking its mesial cusplet. The cusp is moderately high with straight margins and separated lingually from the root by a broad neck. The root is massive, about 12 mm in maximum labiolingual thickness. Its lingual protuberance is not well demarcated. The basal edge of the root is smoothly concave, forming a broad open arch.

WAM 95.7.28 (Pl. 4, figs 8–10); an incomplete 21.5 mm high upper lateral tooth. It lacks a distal cusplet and the distal lobe of the root is broken off. The cusp is curved toward the commissure and its labial face is markedly convex. In occlusal view, the apical half of the cusp is slightly rotated anti-clockwise. The mesial cusplet is rather small, broad-based and with its inner margin at right angles to the base of the mesial edge of the cusp. The neck is broad and well set off from the root by a distinct ridge. As in WAM 95.7.27, the root is bulky.

Comparison. The lower jaw tooth resembles similar-sized lower lateral teeth of *P. tomosus*, but differs, in profile view, by its significantly more slender and slightly lingually curved cusp. Moreover, in *P. tomosus* the labial face of the cusp is perfectly flat whereas in WAM 95.7.27 it is slightly convex.

Remarks. The two teeth are referred tentatively to *Pseudoisurus* but may represent a new genus. Very similar teeth have recently been described from the Turonian of the Western Interior of the USA. Siverson (1992, p. 530) mentioned specimens from Montana (Carlile Shale) and referred them to *Pseudoisurus tomosus*. Williamson *et al.* (1993, p. 456, fig. 6.6–6.9) illustrated another example from the Mancos Shale of Arizona as *Cretolamna woodwardi*. Minor differences between the Australian teeth and the Turonian ones from the USA include a labiolingually thicker cusp and less well developed cusplets in the American teeth.

Family Incertae sedis

Genus PARANOMOTODON Herman *in* Cappetta and Case, 1975

Type species. *Oxyrhina angustidens* Reuss, 1845, from the Turonian of Bohemia.

Remarks. Cappetta and Case (1975) referred *Paranomotodon* to the Alopiidae, which comprises the thresher sharks. There is, however, a major gap in the fossil record between the youngest

Paranomotodon and the oldest *Alopias* Rafinesque, 1810. *Paranomotodon* sp. from the uppermost Campanian (*Nostoceras* (*N.*) *hyatti* Zone) of New Jersey, USA is the youngest record of the genus, whereas *Alopias denticulatus* Cappetta, 1981 from the lower Ypresian of Morocco is the oldest thresher shark.

The genus, *sensu* Herman (1977) and Cappetta (1987), *non* Landemaine (1991), is at present monotypic, comprising only the type species. This is largely due to the poor quality of the type material of that species. Because *P. angustidens* cannot be properly diagnosed using the type material, it is difficult to present formal descriptions of new species diagnosing them critically from the type.

Paranomotodon sp.

Plate 4, figures 11–14

Material. Two teeth from the Thirindine Point ridge; both (WAM 95.7.54–95.7.55) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Description. WAM 95.7.55 (Pl. 4, figs 13–14); a 14 mm high anterior tooth. The cusp is narrow with smooth surfaces. Its labial face is slightly convex with a gentle medio-basal hollow; the lingual face is strongly cambered. The neck is well developed and of equal width (0.7 mm) along the lingual base of the crown. A well-developed lingual protuberance of the root bears a median groove. The tip of the mesial lobe is mesiodistally compressed whereas the extremity of the distal one is flattened labiolingually.

WAM 95.7.54 (Pl. 4, figs 11–12); the second tooth is almost identical to WAM 95.7.55 and possibly from the same file on the opposite side of the symphysis. It differs only in having a mesiodistally compressed extremity of the distal root lobe and in its slightly more robust root.

Remarks. The narrow cusp and almost flat labial face of the crown are features typical for Cenomanian–Turonian examples of the genus. In Campanian *Paranomotodon*, the cusp is broader in anterior teeth and the labial face of the crown is almost as convex as the lingual face.

Genus ANOMOTODON Arambourg, 1952 *sensu lato*

Type species. *Anomotodon plicatus* Arambourg, 1952, from the Maastrichtian of Morocco.

Remarks. Some anterior teeth from very young individuals of *Carcharias* sp. A described below, have short and abrupt, oblique heels instead of cusplets. Moreover, in upper lateral files of juveniles of the same species, cusplets are either very small, barely separated from the heel or absent altogether. The branches of the root are short, not extending laterally beyond the crown. The lateral margins are subvertical with a small central concavity. These juvenile specimens of *Carcharias* sp. A are very similar to the teeth of the late Santonian–Maastrichtian *Anomotodon plicatus*. The latter taxon is the type species of *Anomotodon*. Cappetta (1975) referred *Anomotodon* to the family Mitsukurinidae Jordan, 1898 which comprises the goblin sharks, including the extant genus *Mitsukurina* Jordan, 1898 and the fossil genus *Scapanorhynchus* Woodward, 1889. Cappetta's assignment of *Anomotodon* to the mitsukurinids has found support among other authors, e.g. Case (1980, 1994), Wolberg (1985), Kemp (1991), Landemaine (1991), Long (1992a, 1992b), Siverson (1992), and Biddle (1993). Siverson (1995) tentatively also included *Striatolamia* Glikman, 1964b in the Mitsukurinidae. In my view, the latter genus is probably derived from one of the larger Cretaceous species assigned to *Anomotodon*, e.g. *A. hermani* Siverson, 1992. I have (Siverson 1995), however, questioned the supposed mitsukurinid affinity of *Anomotodon* and, in consequence, *Striatolamia*. While still considering *Anomotodon* to be a true mitsukurinid, Cappetta (1987)

suggested that the genus might be polyphyletic by including species from different lineages. Nevertheless, he believed that *Anomotodon* was probably derived, by loss of the lateral cusplets, from a form dentally similar to the species of *Scapanorhynchus*.

As shown below, juvenile teeth of *Carcharias* sp. A are often close in morphology to the teeth of *A. plicatus*. It is quite possible that the latter evolved through paedomorphic processes operating on the former. Contrary to the opinion of previous authors, I suspect that *A. plicatus* may not be a mitsukurinid and, if that is the case, has to be reassigned to the family Odontaspidae.

As well as the type species, at least seven additional nominal species have been assigned to *Anomotodon* (Long 1992a, Siverson 1992). It is beyond the scope of this paper to review them all but provided my hypothesis on the origin of *A. plicatus* reflects reality, at least the Cretaceous taxa, i.e. *A. principalis*, *A. senessei* (Leriche, 1936) and *A. hermani*, must be assigned to another genus.

‘*Anomotodon*’ sp.

Plate 4, figures 15–16

Material. Six teeth from the Thirindine Point ridge; all of them (WAM 95.7.56, 96.3.32–96.3.36) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Description. Because of the poor state of preservation of the Australian teeth, a detailed description of the dentition of this species is not possible. The teeth do, however, exhibit features typical for Cretaceous species referred to the genus, such as absence of cusplets, a smooth labial face and a folded lingual face of the crown and presence of a median groove on the lingual protuberance of the root.

Remarks. WAM 95.7.56 (Pl. 4, figs 15–16) is a left upper jaw anterior tooth, probably from the third file. It measures 16.0 mm high. The tip of the cusp is missing and the distal part of the only preserved root lobe is somewhat corroded. Originally the tooth was probably about 18 mm high. Considering the size and probable position in the jaw of this specimen and the very small sample of teeth available, it seems certain that the larger teeth from the first or second anterior files of this species reached more than 20 mm in height in old females. The rather large size of the teeth, in combination with heels tapering gradually away from the cusp, indicate a close relationship with the early Campanian ‘A’. *hermani* from Belgium and southern Sweden.

Family ODONTASPIDIDAE Müller and Henle, 1839

Genus JOHNLONGIA gen. nov.

Type species. *Johnlongia allocotodon* gen. et sp. nov.

Derivation of name. After Dr John Long, Western Australian Museum, in recognition of his work on Palaeozoic fishes from Gondwana.

Diagnosis. Anterior teeth with conical cusp, slightly bent towards commissure. Sharp lateral cusplet usually present on mesial or both sides of cusp. Cutting edges continuous and prominent in juveniles; incomplete in adults, often limited to apical third of cusp. Lingual face of crown smooth; labial face basally folded in juveniles but smooth in adults. Root bulky with extremely large and protruding lingual protuberance in adults, divided by deep median groove. Lobes mesiodistally compressed and short, but well separated; mesial one most developed. Two to four well marked lingual marginal foramina open on each side of root.

Lateroposterior teeth labiolingually compressed. Cusp strongly bent toward commissure in upper laterals but more or less erect in lower jaw. Crown may have strong vertical folds on one or both

sides, depending on species, ontogenetic stage and tooth position. Enameloid folds progressively more prominent posteriorly, especially on labial face of crown, and more developed in juveniles than in adults. Crown markedly lingually directed in posterior teeth; its labial face parallel to basal face of root in rearmost teeth. Root distinctly asymmetrical in lateral and posterior teeth of adult individuals with mesial lobe more developed than distal one. Basal face concave, divided by deep and rather broad median groove.

Referred species. *Odontaspis parvidens* Cappetta, 1973, from the Turonian Carlile Shale of South Dakota, USA.

Comparison. The combination of large cusplets in lateral and posterior teeth, a very well marked, deep, median groove on the lingual protuberance of the root in all but some of the extreme posterior files, and strong labial folds, at least in the posterior half of the dentition, sets *Johnlongia* gen. nov. apart from all other lamniform genera except for those of the family Odontaspidae. The common absence of a distal cusplet on anterior teeth from adult individuals, cutting edges confined to the tip of the cusp and a root with an enormous lingual protuberance and short mesiodistally compressed branches are features each of which separates *Johnlongia* gen. nov. from all other genera of Odontaspidae.

Remarks. The genus is also present in the Albian of Queensland (Noel Kemp and David Ward. pers. comm.) and possibly in the Turonian of New Mexico (see Wolberg 1985).

Johnlongia allocotodon gen. et sp. nov.

Plate 5, figures 1–15; Text-figure 5A–F

Derivation of the name. Combination of the Greek *allocotus* (of unusual form) and *odus* (tooth).

Holotype. Lower lateral tooth, WAM 95.9.1; Plate 5, figures 8–9; Thirindine Point ridge (eastern slope); basal 0.1 m of Beedagong Claystone.

Paratypes. WAM 95.9.2–WAM 95.9.10; Plate 5, figures 1–7, 10–15, Text-figure 5A–F.

Additional material. 120 teeth from the Thirindine Point ridge; 100 of these are from the basal 0.1 m of the Beedagong Claystone (WAM 96.3.43 [40 teeth] and 96.3.44–96.3.48, 96.3.49–96.3.53 [three teeth each], 96.3.54–96.3.55 [five teeth each] and 96.3.56–96.3.58 [ten teeth each]), 14 teeth are from 0.15–0.35 m above the base of the Beedagong Claystone (WAM 96.3.59–96.3.61 [12 teeth]) and six teeth were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone (WAM 96.3.37–96.3.42).

Diagnosis. Anterior teeth with smooth enameloid in adults; basal half of labial face of crown with strong vertical folds in juveniles. Cutting edges incomplete in teeth of adults, usually limited to apical third or so of cusp. Distal edge in distolingual position on anteriormost teeth. In juveniles, cutting edges strong and continuous, reaching base of cusp. Lingual protuberance of root progressively more protruding with age.

Lateral teeth labiolingually compressed. Cusp strongly bent towards commissure in upper jaw teeth; more or less erect in lower jaw. Lingual face of crown usually smooth in adults but folded in juveniles. Labial face with strong vertical folds, often relatively short and widely spaced in adults.

Posterior teeth less differentiated between upper and lower jaw than laterals. Lingual face of crown with well-marked folds. Labial folds progressively stronger posteriorly through files. Rearmost teeth display simple root, sometimes lacking median groove.

Description. Anterior teeth reach at least 8.5 mm high. In adult individuals, the enameloid of the crown is smooth. The cusp is conical, sigmoidal in profile and slightly bent toward the rear. Narrow, pointed lateral

cusplets are present on the mesial or both sides of the cusp but occasionally anterior teeth of adults are devoid of cusplets. The cutting edges, more developed on the mesial side, are usually incomplete in teeth from adult individuals, often limited to the apical third of the cusp. The distal cutting edge is in a distolingual position on anteriormost teeth. The root is very large relative to the crown and features an extremely bulky and protruding lingual protuberance (Pl. 5, fig. 2) divided by a deep median groove. The lobes are short, mesiodistally compressed, but well separated.

Upper lateral teeth have a distinctly commissurally bent cusp (Pl. 5, fig. 11). The crown is relatively wider than in anterior teeth and bears one or two cusplets on each side of the cusp. Lingually, the crown is cambered, smooth or with folded enameloid. When present, lingual folds are usually well-marked. The labial face of the cusp is convex but less so than the lingual side. There are strong but sometimes sparsely spaced labial folds, relatively shorter in adults. The root is very asymmetrical in adults, with a much longer mesial extremity, and labiolingually compressed with a slightly concave basal face divided by a prominent deep median groove.

Lower lateral teeth (Pl. 5, figs 8–9) feature an erect cusp and almost symmetrical crown, but are otherwise as upper laterals.

Posterior teeth are of similar morphology in both jaws. The cusp is lower and more lingually directed than in laterals. There is one pair of lateral cusplets. Labial folds are very coarse (Pl. 5, fig. 12); lingual ones are finer (Pl. 5, fig. 13). The lobes are progressively less well differentiated from the rest of the root posteriorly through the files. The rearmost teeth may lack a median groove on the lingual protuberance of the root.

There is a very marked ontogenetic heterodonty in anterior files of this species, with teeth from juveniles displaying prominent and continuous cutting edges and strong labial folds on the basal half of the crown, as opposed to the incomplete cutting edges and smooth enameloid in adults. Moreover, the lingual protuberance of the root is less protruding in juveniles (Pl. 5, figs 4–7). In lateral files, teeth of juveniles are more robust (Text-fig. 5A–F), with a more symmetrical root and much stronger folds on the crown than those of adults (Pl. 5, figs 8–11).

Comparison. According to Cappetta (1973, p. 507), the distal cutting edge on anterior teeth of *J. parvidens* is either restricted to near the tip of the cusp or missing altogether. All examined anterior teeth of *J. allocotodon* do possess a distal edge although it is limited to approximately the apical third of the cusp. In juveniles of the latter, the cutting edges are strong and continuous on anterior teeth. The labial face of the crown is smooth in lateral teeth of *J. parvidens* whereas in *J. allocotodon* there are strong, but sometimes sparsely spaced, labial folds along the base of the crown. Unfortunately, the description and illustrations of the dentition of *J. parvidens* do not include teeth from the posterior half of the tooth row. Cappetta (1973) noted a maximum tooth height of 6 mm in his sample of *J. parvidens*, whereas the largest examined tooth of *J. allocotodon* is considerably larger at 8.5 mm.

Genus *CARCHARIAS* Rafinesque, 1810

Type species. *Carcharias taurus* Rafinesque, 1810, extant, on the shelves in temperate and tropical seas; usually in shallow, inshore waters.

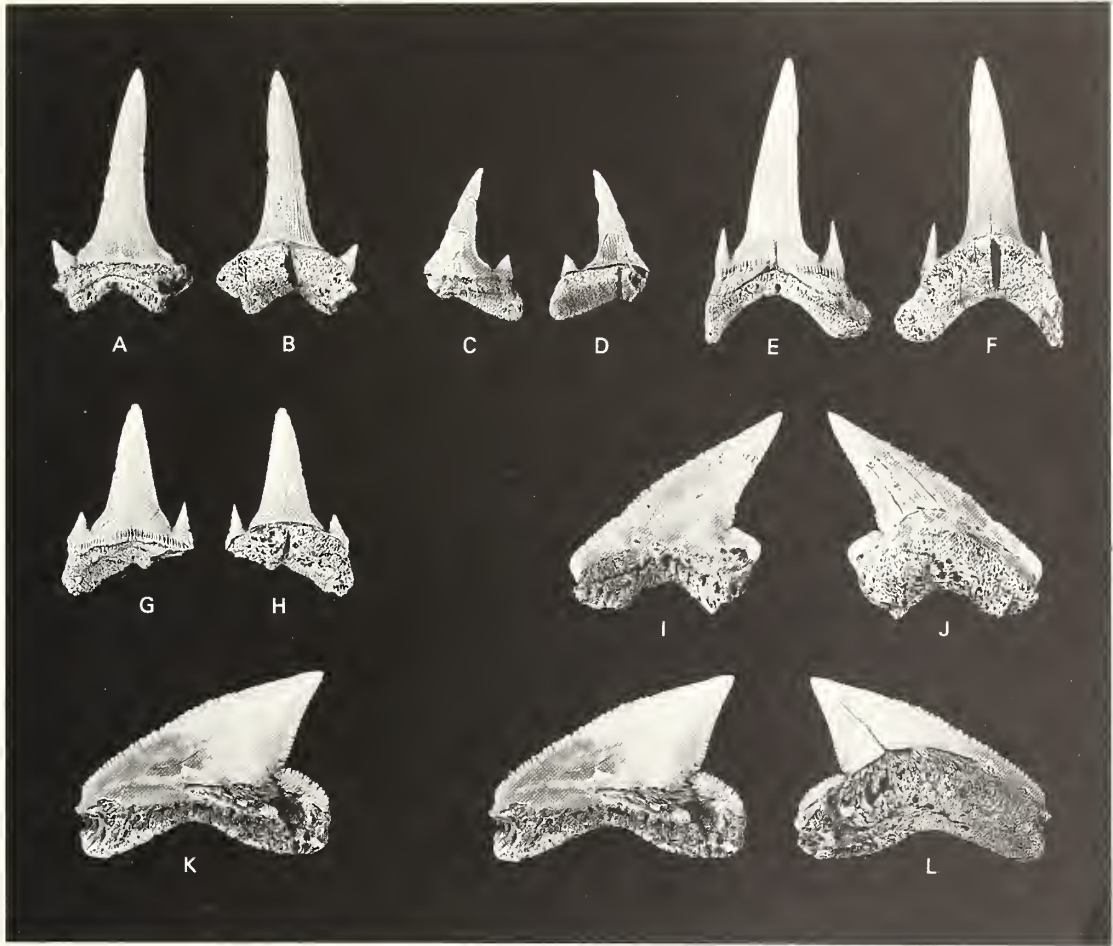
EXPLANATION OF PLATE 5

Figs 1–15. *Johnlongia allocotodon* gen. et sp. nov. 1–3, WAM 95.9.2, paratype; 7.4 mm high anterior tooth from an adult individual, labial, profile and lingual view; $\times 7.7$. 4–6, WAM 95.9.3, paratype; 4.9 mm high anterior tooth from a juvenile individual, labial, profile and lingual view; $\times 9.5$. 7, WAM 95.9.94, paratype; 3.0 mm high anterior tooth from a very young individual, lingual view; $\times 9.7$. 8–9, WAM 95.9.1, holotype; 6.1 mm high lower lateral tooth from an adult individual, lingual (stereo pair) and labial (stereo pair) view; $\times 8.3$. 10–11, WAM 95.9.5, paratype; 3.4 mm high upper lateral tooth from an adult individual, lingual and labial view; $\times 9.6$. 12–13, WAM 95.9.6, paratype; 1.3 mm high posterior tooth from an adult individual, labial and lingual view; $\times 22$. 14–15, WAM 95.5.7, paratype; 1.2 mm high commissural tooth, lingual and labial view; $\times 22$. All teeth from the basal 0.1 m of the Beedagong Claystone (78 kg sample), Thirindine Point east.





TEXT-FIG. 5. A-F, *Johnlongia allocotodon* gen. et sp. nov. A-B, WAM 95.9.8; paratype; 1.4 mm high upper lateral tooth, lingual and labial view. C-D, WAM 95.9.9; paratype; 1.4 mm high lower lateral tooth, lingual and labial view. E-F, WAM 95.9.10; paratype; 1.7 mm high ?lower lateral tooth, labial (stereo pair) and lingual (stereo pair) view. G-J, *Carcharias* sp. A. G-H, WAM 95.9.11; 6.6 mm high anterior tooth, labial and lingual view. I-J, WAM 95.9.12; 3.6 mm high upper lateral tooth, lingual (stereo pair) and labial view. A-F from the basal 0.1 m of the Beedagong Claystone (78 kg sample); all $\times 22$; G-J from the middle third of the Beedagong Claystone (80 kg sample); both $\times 8.7$. All teeth in the text-figure are from juvenile individuals.



TEXT-FIG. 6. A-D, *Carcharias* sp. A. A-B, WAM 95.7.57; 11 mm high lower ?anterior tooth (LA3?), both lobes of the root and one cusplet broken off, labial and lingual view; Thirindine Point east. C-D, WAM 95.7.58; 6.5 mm high upper right lateral tooth, mesial root-lobe and cusplet broken off, labial and lingual view; Thirindine Point east. E-H, *Carcharias* sp. B. E-F, WAM 95.7.59; 13 mm high upper right anterior tooth (UA2), mesial lobe of root poorly preserved, labial and lingual view; Thirindine Point east. G-H, WAM 95.7.60; 8 mm high lower lateral tooth, root poorly preserved, labial and lingual view; Thirindine Point east. I-L, *Squalicorax* ex gr. *curvatus* (Williston, 1900). I-J, WAM 95.7.61; 9.5 mm wide anterolateral tooth, labial and lingual view; Thirindine Point west. K-L, WAM 95.7.62; 11.3 mm wide lateral tooth, labial (stereo pair) and lingual view; Thirindine Point east. All $\times 3$.

Carcharias sp. A

Text-figures 5G-J, 6A-D

Material. 137 teeth from the Thirindine Point ridge; 76 of these are from the basal 0.1 m of the Beedagong Claystone (WAM 96.3.62-96.3.63 [two teeth each], 96.3.64 [12 teeth], 96.3.65-96.3.68 [15 teeth each]), 50 teeth are from 0.15-0.35 m above the base of the Beedagong Claystone (WAM 95.9.11-95.9.12, 96.3.69, 96.3.70, 96.3.71-96.3.72 [15 teeth each] and 96.3.73 [16 teeth]) and 11 teeth were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone (WAM 95.7.57-95.7.58, 96.3.74-96.3.82).

Additional occurrences. The *Mantelliceras dixonii* and/or *Turrilites costatus* Zone/Subzone of Germany (described as *Eosriatolamia? subulata* by Müller and Diedrich 1991).

Description. Anterior teeth, reaching at least 14.5 mm high (incomplete tooth), with one pair of small, sharp lateral cusplets. Some of the juvenile teeth have short oblique heels instead of well-defined cusplets. Upper lateral teeth are bent toward the commissure, whereas lower laterals are almost symmetrical with an erect cusp. There is one pair of triangular cusplets in lateral teeth from adults. In juveniles, cusplets are often poorly developed (Text-fig. 5I–J) or absent. In the latter case the teeth have low, abruptly terminating heels. Posterior teeth are strongly distally directed and usually lack cusplets. The labial face of the cusp is flat to slightly convex in anterior teeth; it becomes progressively more convex posteriorly so that in posterior teeth the lingual and labial faces are equally convex. All anterior teeth have strong flexuous lingual folds. In lateral and posterior teeth the folds are often less conspicuous or may even be missing altogether. Lingual folds are roughly equally dense in all teeth so that the number of folds increases with tooth size. In anterior and most lateral teeth the labial face is completely smooth. In posterior and some lateral teeth there are short basal folds. The labial face of the crown does not overhang the root in lateral teeth and the basal face of the root is flat to slightly concave. Root branches are very short in juveniles, not extending much beyond the crown. Also, in young individuals the marginal edges of the root are subvertical with a small central concavity. In adults the extremities of the root are longer, extending well beyond the crown.

Remarks. See the discussion on *Anomotodon*.

Carcharias sp. B

Text-figure 6E–H

Material. Two teeth from the Thirindine Point ridge; both (WAM 95.7.59–95.7.60) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Description. WAM 95.7.59 (Text-fig. 6E–F); a 13 mm high, second upper right anterior tooth. The cusp is high, slender, sigmoid in profile and possesses continuous cutting edges. There is one pair of high cusplets, parallel to the cusp. The lingual face of the cusp bears a few, weak folds. The labial face of the crown has short, but strong vertical folds along its base. The lingual protuberance of the root is divided by a distinct median groove. The distal extremity of the root is labiolingually compressed, whereas the mesial lobe, which lacks its tip, is more slender and much less flattened.

WAM 95.7.60 (Text-fig. 6G–H); an 8 mm high, imperfectly preserved lower lateral tooth. The cusp is erect with a completely smooth lingual face. Short, prominent labial folds are present along the base of the crown. There is one pair of rather high and slender cusplets.

Comparison. The short but strong labial folds along the base of the crown, relatively high cusplets and more or less smooth lingual face of the crown are features each of which separates this species from *Carcharias* sp. A.

EXPLANATION OF PLATE 6

Figs 1–12. *Squalicorax volgensis* (Glikman in Glikman and Shvazhaite, 1971). 1–2, WAM 95.9.13; 7.2 mm wide anterolateral tooth, lingual and labial view; surface-collected but probably from the lower part of the Beedagong Claystone. 3–4, WAM 95.9.14; 6.4 mm wide lateral tooth, lingual and labial view; basal 0.1 m of the Beedagong Claystone (78 kg sample). 5–6, WAM 95.9.15; 5.8 mm wide anterolateral tooth, lingual and labial view; surface-collected from the uppermost metre of the Alinga Formation or the basal Beedagong. 7–8, WAM 95.9.16; 7.0 mm wide lateral tooth, lingual and labial view; basal 0.1 m of the Beedagong Claystone (78 kg sample). 9–10, WAM 95.9.17; 6.4 mm wide anterolateral tooth, lingual and labial view; basal 0.1 m of the Beedagong Claystone (78 kg sample). 11–12, WAM 95.9.18; 6.1 mm wide anterolateral tooth, lingual and labial (stereo pair) view; surface-collected but probably from the lower part of the Beedagong Claystone. All from Thirindine Point east; $\times 6.3$.



SIVERSON, *Squalicorax volgensis*

Family ANACORACIDAE Casier, 1947

Remarks. Prior to this publication, Australian records of squalicoracids were confined to a single tooth from the Albion of north-central Queensland, possibly the Toolebuc Formation, figured as *Pseudocorax australis* by Kemp (1991, pl. 4, fig. m). He also illustrated (pl. 4, figs n–w), under the same name, ten teeth of a typical echinorhinid, possibly *Echinorhinus* de Blainville, 1816. The species *australis* was originally described by Chapman (1909) from the Toolebuc Formation (see Pledge 1992, p. 17) of the Eromanga Basin, Queensland, and referred by him to *Corax* (= *Squalicorax*). Pledge (1992) correctly pointed out that *Corax australis* is not a squalicoracid and should be reassigned to the echinorhinids.

Genus SQUALICORAX Whitley, 1939

Type species. *Corax pristodontus* Agassiz, 1843, from the Maastrichtian of Maastricht, Holland.

Squalicorax ex gr. *curvatus* (Williston, 1900)

Text-figure 6i–L

Material. Nine teeth from the Thirindine Point ridge; all of them (WAM 95.7.61–95.7.62, 96.3.83–96.3.89) were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone.

Description. The two selected teeth described below are the best preserved ones from Thirindine Point.

WAM 95.7.62 (Text-fig. 6k–L); an 11.3 mm wide ?upper lateral tooth. The cusp is triangular and distally directed. All cutting edges have strong serrations. The mesial cutting edge is gently convex, whereas the distal edge is slightly concave. The distal heel is gently convex and well detached from the distal edge of the cusp. Labially, the crown overhangs the root medially by a distinct bulge. Several foramina open along the labial face of the root, just below the crown. The labial face of the cusp is gently convex but the labial face of the tooth as a whole is concave.

WAM 95.7.61 (Text-fig. 6i–j); a 9.5 mm wide anterolateral tooth. The distally directed cusp is elongated and narrow with a slightly convex mesial edge and a gently concave distal edge. Serrations are somewhat poorly preserved due to corrosion. The labial face of the crown overhangs the root medially, but not as markedly as in WAM 95.7.62. Both extremities of the root are incomplete.

Remarks. WAM 95.7.62 is close in morphology to one of the two teeth comprising the type series of *Corax curvatus* (Williston, 1900, pl. 30, fig. 8). Cenomanian squalicoracids have otherwise commonly been assigned to Agassiz's *Corax falcatus*, e.g. Woodward (1912), Herman (1977), Sokolov (1978), Cappetta (1987) and Müller and Diedrich (1991). It is obvious that '*C.*' *falcatus* is based on more than one species. The teeth in Agassiz's plate 26a, respectively figures 5 and 8–11, are examples of two different squalicoracids both included in this nominal species. One (fig. 5) is typical of the *S. kaupi* group with its large serrations and characteristic labial ridge, stretching from the tip of the cusp down medially toward the base of the crown. The others (figs 8–11) are of the same type as the Texan material figured as *S. falcatus* by Welton and Farish (1993). Typical dental features include a strikingly flat labial face of the crown in adults, an often convex distal edge of the cusp, and a straight to gently convex mesial edge of the cusp. Furthermore, the serrations are usually finer and the cusp is more erect than in coeval species of the *S. kaupi* group.

Glikman (1980, p. 107) chose the tooth in Agassiz's plate 26a, figure 1 as the lectotype for *Corax falcatus*. This specimen, now being the fixed standard of *S. falcatus* (see the ICZN article 74a in Ride *et al.* 1985, p. 153), differs significantly from the Western Australian teeth in two important aspects. First, the labial face of the root is medially much higher in *S. falcatus*. Secondly, in the Alinga Formation/Beedagong Claystone teeth the base of the labial face of the crown overhangs the root medially by a distinct bulge, whereas in the lectotype of *S. falcatus* the root and the crown appear to be flush in the same plane labially.

Squalicorax volgensis (Glikman *in* Glikman and Shvazhaite, 1971)

Plate 6, figures 1–12

- * 1971 *Palaeoanacorax volgensis* Glikman *in* Glikman and Shvazhaite, p. 187, pl. 1, figs 5–6, (?non fig. 7).
- ?1980 *Palaeoanacorax volgensis* (Glikman); Glikman, p. 97, pl. 13, fig. 18.
- .1991 *Pseudocorax primulus* Müller and Diedrich, p. 40, pl. 22, figs 1–5.
- .1993 *Squalicorax* sp.; Welton and Farish, p. 120, figs 1–2.

Material. One hundred teeth from the Thirindine Point ridge; 56 of these are from the basal 0.1 m of the Beedagong Claystone (WAM 95.9.14, 95.9.16–95.9.17, 96.3.90–96.3.100, 96.3.101 [two teeth] and 96.3.102–96.3.105 [ten teeth each]), ten teeth are from 0.15–0.35 m above the base of the Beedagong Claystone (WAM 96.3.106, 96.3.107 and 96.3.108 [eight teeth]) and 34 teeth were surface-collected from approximately the uppermost metre of the Alinga Formation and/or the basal part of the Beedagong Claystone (WAM 95.9.13, 95.9.15, 95.9.18, 96.3.109–96.3.113 [five teeth each] and 96.3.114 [six teeth]).

Additional occurrences. *Actinocamax primus* Zone of the Saratov Province, Russian Platform; within the *Mantelliceras dixonii* to *Turrillites costatus* Zone/Subzone interval of Ascheloh, Teutoburger Wald, north-west Germany; Weno Formation (late Albian), Tarrant County, Texas, USA; and possibly in beds yielding *Turrillites costatus* of the Bakhchisaraj region of the Crimean Range, Ukraine (Naidin 1981, species list only).

Description. The teeth are of moderate size, not exceeding about 9 mm wide in the Western Australian population. The cusp is sub-erect to erect in anterior files. It is progressively more distally bent posteriorly. The mesial edge of the crown is straight, slightly convex or sigmoid. Cutting edges are usually more or less smooth, but teeth with irregularly developed serrations are not uncommon. The labial face of the cusp is usually very flat in adults (Pl. 6, figs 11–12, stereo pair). In some teeth the lingual neck, separating the crown from the root, displays short vertical hollows separated by ridges (Pl. 6, fig. 3; compare Welton and Farish 1993, p. 120, fig. 2a). The crown overhangs the root labially by a distinct median bulge. Lobes of the root are well separated due to a deeply notched basal edge.

Remarks. For a given category of teeth, there is a considerable degree of heterodonty in this species. Whether this heterodonty is mainly of a dignathic or gynandric nature remains to be determined. Unlike several other species of shark, there does not appear to be any clear-cut correlation between the ontogenetic stage of the tooth and the onset of development of serrations in *S. volgensis*.

When Glikman (*in* Glikman and Shvazhaite 1971) first described the species *volgensis*, he made it the type of the new nominal genus *Palaeoanacorax*. Cappetta (1987, p. 109) synonymized *Palaeoanacorax* with *Squalicorax*. This conservative taxonomic approach is applied here. However, it is quite possible that future work will demonstrate that *S. volgensis* is indeed generically distinct from coeval members of *S. ex gr. curvatus*.

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THE AMMONITE *SUTNERIA* FROM THE UPPER JURASSIC OF SOUTHERN SPAIN

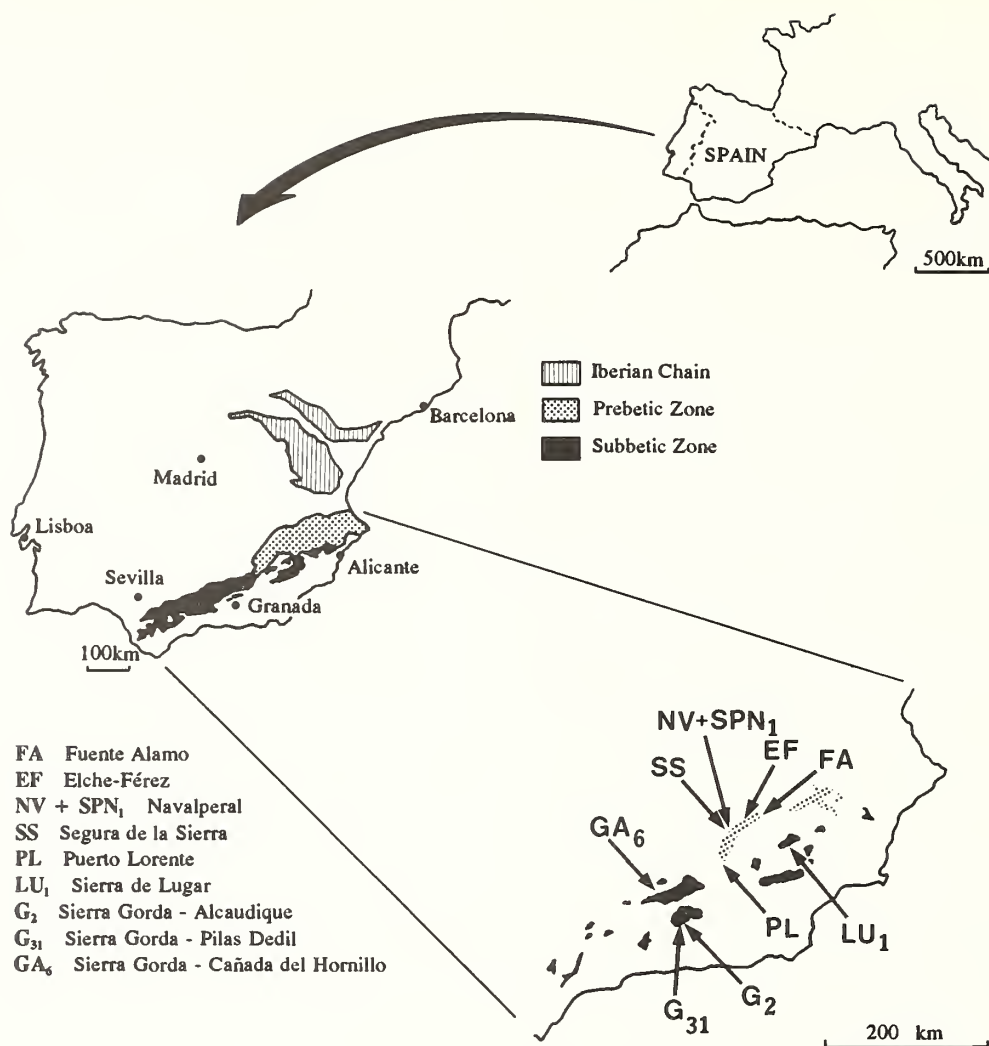
by F. OLÓRIZ and F. J. RODRÍGUEZ-TOVAR

ABSTRACT. A bed-by-bed collection of 144 specimens of the ammonite genus *Sutneria* from the uppermost Oxfordian and lowermost Kimmeridgian of southern Spain comprises the species and subspecies *galar* Oppel, *galar thieli* Zeiss, *nusplingensis* Fischer and *platynota* Reinecke. These represent the most complete assemblage of the genus known from the western Tethys. All the species, except *nusplingensis*, were found in epicontinental facies (alternating marls, marly limestones and limestones) as well as in epiocceanic facies (*ammonitico rosso*). *S. nusplingensis* occurs only rarely at the base of the epicontinental Kimmeridgian. *S. galar thieli* ranges from the upper Planula Zone of the Upper Oxfordian to the Platynota Zone of the Lower Kimmeridgian. *S. galar* and *S. platynota*, by far the most common species, show their normal stratigraphical distribution in the uppermost Oxfordian and lower Kimmeridgian, respectively; this reinforces their usefulness for correlation in the European Tethys and surrounding areas.

THE genus *Sutneria* Zittel, 1884 comprises small ammonites normally included in the subfamily Aulacostephaninae Spath, 1924 (e.g. Arkell *et al.* 1957; Barthel 1959; Geyer 1961; Schairer 1970; Contini and Hantzpergue 1975), although classification at this systematic level is still open to discussion (Berckhemer and Hölder 1959; Olóriz 1978; Zeiss 1979; Callomon *in* Donovan *et al.* 1981). These ammonites develop bifurcate, polygyrate and even fasciculate ribbing on their planulate or globose shells, and only rarely exhibit tubercles. In the uppermost Kimmeridgian and Lower Tithonian, only slightly ornamented or almost smooth forms are known. In Submediterranean Europe and on the northern margin of the westernmost Tethys, *S. galar* (Oppel) and *S. platynota* (Reinecke) are valuable biostratigraphical markers characterizing, respectively, the youngest subzone of the Oxfordian and the oldest zone of the Kimmeridgian. Previously, these two species have been recognized most often in Submediterranean ammonite assemblages, with less well documented records from more southerly regions. In the Iberian Peninsula (Text-fig. 1), outside the Betic Cordillera, one or both of these species have been found in the Iberian Chain (Geyer 1966, 1969; Meléndez *et al.* 1983, 1990; Moliner 1983; Atrops and Meléndez 1984; Moliner and Olóriz 1984) and in Portugal (Marques 1983; Atrops and Marques 1986, 1988; Rodríguez-Tovar 1993). In the Betic Cordillera, *S. platynota* (Reinecke) and/or *S. galar* (Oppel) have been cited by Behmel (1970), Fourcade (1970, 1971), Azéma *et al.* (1971), López-Garrido (1971), Azéma (1977), Olóriz (1978, 1979), Sequeiros and Olóriz (1979), García-Hernández *et al.* (1979, 1981), Rodríguez-Tovar (1990, 1993), Olóriz *et al.* (1991, 1992), López-Galindo *et al.* (1992) and Olóriz and Rodríguez-Tovar (1993a, 1993b). Although the genus has been known in southern Spain for many years, only the recent papers of the present authors established its moderate abundance in the uppermost Oxfordian and lowermost Kimmeridgian, and recent research has extended the biogeographical range of the more common species.

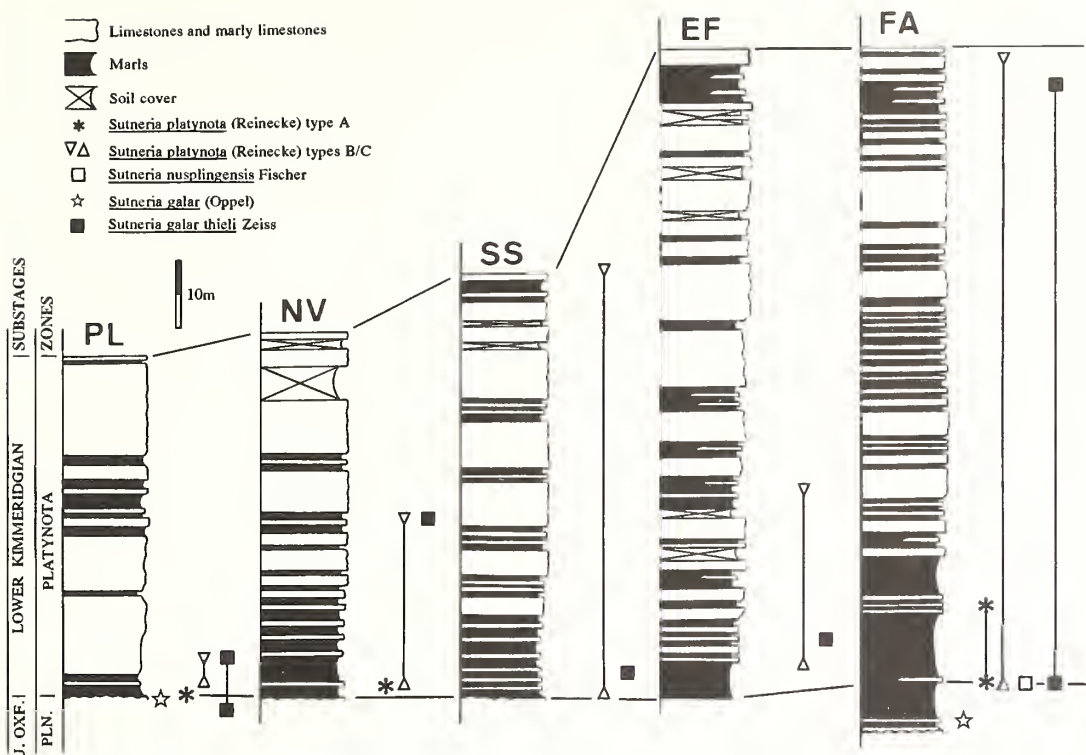
SECTIONS STUDIED AND STRATIGRAPHICAL REMARKS

A total of 142 specimens of *Sutneria* was collected by the authors from nine sections in southern Spain (Text-fig. 1). These are Fuente Alamo (FA) (sheet 26–32, Montealegre del Castillo: 1°25'20" W, 38°41'45" N), Elche-Férez (EF) (sheet 24–34, Elche de la Sierra: 2°00'10" W,

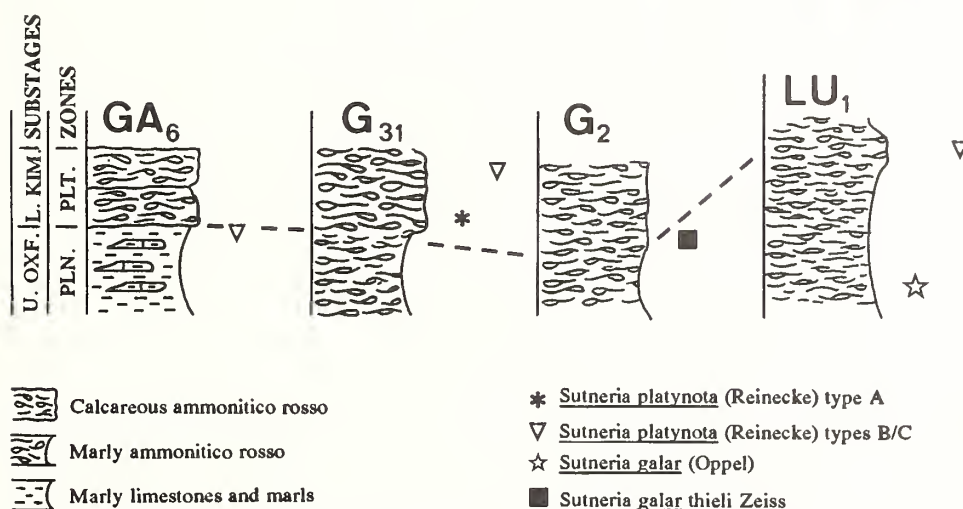


TEXT-FIG. 1. Upper Jurassic outcrops in southern Spain. Subbetic Zone (black), Prebetic Zone (stippled). Sections: Sierra Gorda-Alcaudique (G₂), Sierra Gorda-Pilas Dedil (G₃₁), Sierra Gaena-Cañada del Hornillo (GA₆), Sierra de Lugar (LU₁), Puerto-Lorente (PL), Segura de la Sierra (SS), Navalperal (NV and SPN₁), Elche-Férez (EF), Fuente Alamo (FA).

38°23'20" N), Navalperal (NV) and (SPN₁) (sheet 22–35, Orcera: 2°37'00" W, 38°18'30" N), Segura de la Sierra (SS) (sheet 22–35, Orcera: 2°38'25" W, 38°18'05" N), Puerto Lorente (PL) (sheet 21–37, Cazorla: 2°59'25" W, 37°50'15" N), Sierra Gorda-Alcaudique (G₂) (sheet 18–42, Loja: 4°8'25" W, 37°7'53" N), Sierra Gorda-Pilas Dedil (G₃₁) (sheet 18–42, Loja: 4°3'13" W, 37°2'57" N), Sierra de Gaena-Cañada del Hornillo (GA₆) (sheet 17–40, Lucena: 4°18'48" W, 37°25'20" N), and Sierra de Lugar (LU₁) (sheet 27–35, Fortuna: 1°10'45" W, 38°12'49" N). Sheet numbers refer to the 1:50000 topographical series. In addition, two specimens of *S. platynota* (Reinecke) were collected from the lower part of two other sections with poorly exposed or ammonite-poor Kimmeridgian strata. This collection of 144 specimens is by far the most complete *Sutneria* assemblage known from the uppermost Oxfordian and the lowermost Kimmeridgian in the western Tethys.



TEXT-FIG. 2. Lithologies, ammonite distribution and stratigraphy of the studied sections in epicontinental areas.



TEXT-FIG. 3. Lithologies, ammonite distribution and stratigraphy of the studied sections in epi-oceanic areas. Scale bar represents 0.2 m.

Text-figures 2–3 show the stratigraphical distribution of species in the sections analysed. It is noteworthy that *S. platynota* was recorded in two relatively close but extremely different eco-sedimentary environments having, for example, enormous thickness differences for equivalent

bio-chronostratigraphical intervals. In the epicontinental Prebetic (sections PL, SS, NV, EF and FA), comparatively extended successions of the Puerto Lorente Formation (Pendas 1971) mainly comprise alternating limestones and marls, and are relatively poor in ammonites. Differences in *Sutneria* records obtained in these areas are not clearly related to lithology. In the epioceanic Subbetic (sections G₂, G₃₁, GA₆ and LU₁), ammonite-rich nodular limestones belonging to the Ammonitico Rosso Superior Formation (Molina 1987) show comparatively extreme stratigraphical condensation, and represent the typical deposits in distal pelagic swells in the Tethys.

SYSTEMATIC PALAEONTOLOGY

Location of specimens. All the specimens studied are in the collections of the Departamento de Estratigrafía y Paleontología of the University of Granada (Spain) with catalogue numbers prefixed PL, SS, SPN, RG-CH, BU, FA, EF, FLU, FG, FGA, and ZG.

Conventions. Dimensions are given in millimetres for only those specimens for which complete measurements were possible. Dm = maximum diameter; Wb = whorl breadth; Wh = whorl height; U = umbilicus; U/D = umbilicus:shell diameter ratio; Wb/D = whorl breadth:shell diameter ratio; FTD = diameter at the first external tubercle; LTD = diameter at the last external tubercle; UR/2 = number of umbilical ribs per half whorl; VR/2 = number of ventral ribs per half whorl; T = number of external tubercles; PLTUR = number of umbilical ribs after the last external tubercle; RI = rib index or the number of ventral ribs per ten umbilical ribs.

Order AMMONOIDEA Zittel, 1884

Suborder AMMONITINA Hyatt, 1889

Superfamily PERISPHINCTACEAE Steinmann *in* Steinmann and Doderlein, 1890

Family AULACOSTEPHANIDAE Spath, 1924

Subfamily AULACOSTEPHANINAE Spath, 1924

Genus SUTNERIA Zittel, 1884

Type species. *Nautilus platynotus* Reinecke, 1818. Neotype, from Ützing, North Franconia, Germany, designated by Geyer (1961 p. 131, pl. 3, fig. 11).

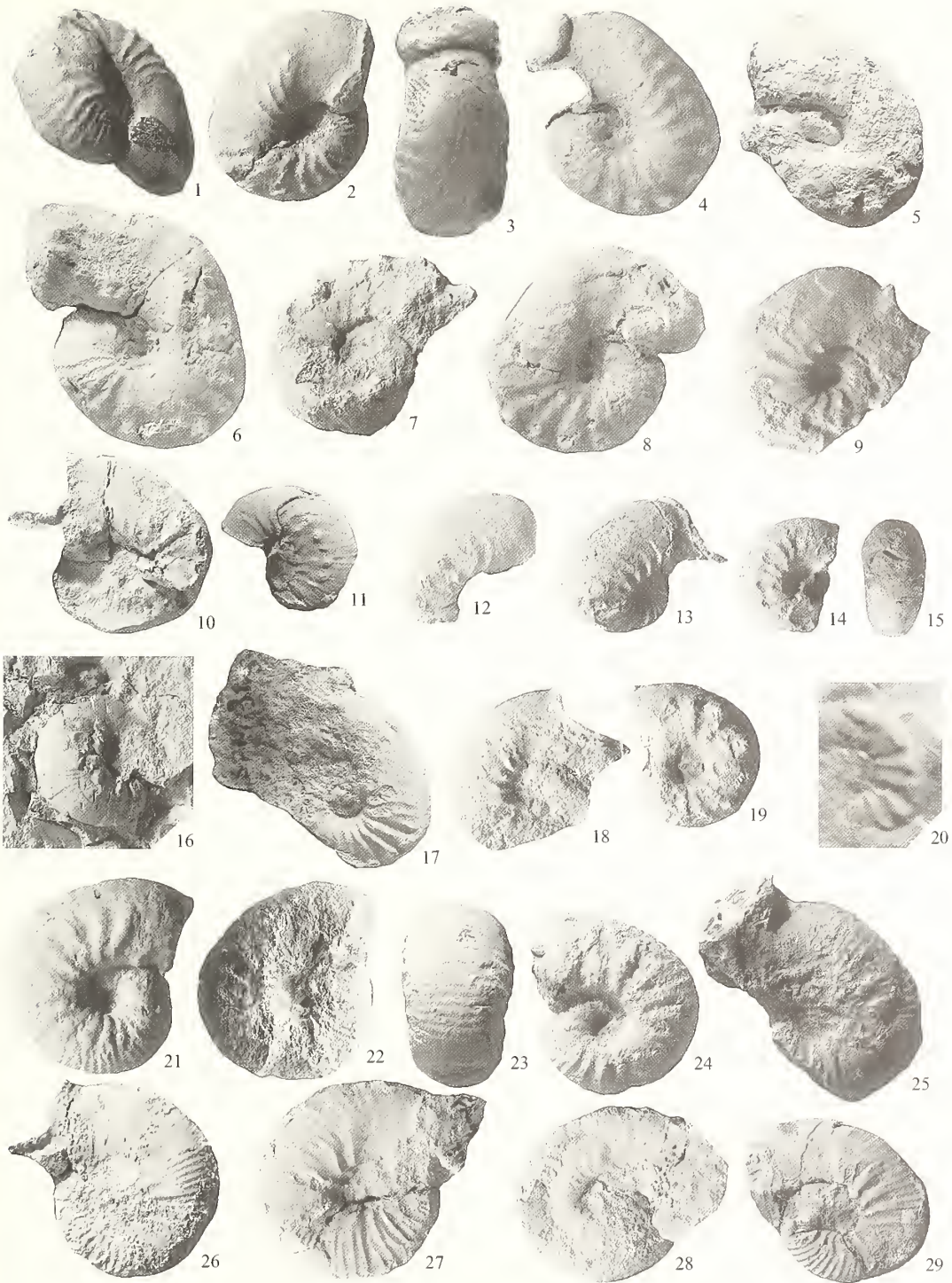
EXPLANATION OF PLATE 1

Figs 1–20. *Sutneria platynota* (Reinecke, 1818); microconchs; Platynota Zone. 1–2, F.LU₁.G.2; morphotype B; Sierra de Lugar; Bed G. 3–4, F.LU₁.G.3; morphotype C; Sierra de Lugar; Bed G. 5, F.GA₆/7.1; morphotype B/C; Sierra de Gaena-Cañada del Hornillo; boundary between Beds 6 and 7. 6, F.LU₁.G.1; morphotype B/C; Sierra de Lugar; Bed G. 7, NV-o.1; morphotype A; Navalperal; Bed O. 8, F.LU₁.G.4; morphotype B/C; Sierra de Lugar; Bed G. 9, FA-75.59; morphotype A/B; Fuente Alamo; Bed 75. 10, SS-(30)19A.1; morphotype B; Segura de la Sierra; 0.3 m below Bed 19A. 11, SPN₁-33.2; morphotype C; Navalperal; Bed 33. 12, EF-6.1; morphotype B; Elche-Ferez; Bed 6. 13, SS-4.9; morphotype B/C; Segura de la Sierra; Bed 4. 14–15, PL-HG.C.3; morphotype A; Puerto Lorente; ferruginized surface beneath alternating marls, marly limestones and limestones. 16, FA-6.90; morphotype A; Fuente Alamo; Bed 6. 17–18, SPN₁-31.6; morphotype C; Navalperal; Bed 31. 19, PL-HG.C.2; morphotype A; Puerto Lorente; ferruginized surface beneath alternating marls, marly limestones and limestones. 20, FA-53.1; Fuente Alamo; Bed 53.

Figs 21–29. *Sutneria galar* (Oppel, 1863); microconchs; Planula Zone (Galar Subzone). 21, München AS VIII 34; original (cast) figured by Oppel (1863, pl. 67, fig. 5) and designated lectotype by Barthel (1959, p. 59, pl. 6, figs 8–9); Thalmässing (Mfr.); 'Weisser Jura β_2 , 22, F.LU₁.G(30–35).1; Sierra de Lugar; 0.3–0.35 m below Bed G. 23–24, PL-HG.C.1; Puerto Lorente; ferruginized surface beneath alternating marls, marly limestones and limestones. 25, PL-HG.C.100; Puerto Lorente; ferruginized surface beneath alternating marls, marly limestones and limestones. 26, FA-4.201; Fuente Alamo; Bed 4. 27, FA-4.19; Fuente Alamo; Bed 4. 28, FA-4.201; Fuente Alamo; Bed 4. 29, FA-4.237; Fuente Alamo; Bed 4.

Bed numbers follow Olóriz (1978) and Rodríguez-Tovar (1993).

All $\times 1.5$.



Sutneria platynota (Reinecke, 1818)

Plate 1, figures 1–20; Text-figure 4

- 1818 *Nautilus platynotus* Reinecke, p. 72, pl. 4, figs 41–42.
 1877 *Ammonites* (*Perisphinctes*) *platynotus*, Reinecke; Favre, p. 47, pl. 5, fig. 2.
 1878 *Ammonites* (*Perisphinctes*) *platynotus*, Reinecke; de Loriol, p. 91, pl. 15, figs 1–2.
 non 1878 *Perisphinctes platynotus* Reinecke; Herbich, p. 166, pl. 11, fig. 2.
 1886 *Ammonites platynotus* (Reinecke); Pillet, p. 10, pl. 1, figs 9–12.
 1887–88 *Ammonites platynotus* Reinecke; Quenstedt, p. 999, pl. 112, fig. 6.
 1887–88 *Ammonites reineckianus* Quenstedt, p. 1001, pl. 112, figs 7–14, 18 (?15, non 16–17); p. 1020, pl. 116, fig. 14.
 1961 *Sutneria* (*Sutneria*) *platynota* (Reinecke); Geyer, p. 131, pl. 3, figs 11–12.
 1964 *Sutneria platynota* (Rein.); Hölder, p. 242, fig. 73–3.
 1969 *Sutneria platynota* (Reinecke); Geyer, p. 65, fig. 1.
 1970 *Sutneria* (*Sutneria*) *platynota* (Reinecke); Schairer, p. 155, pl. 1, figs 1–12; pl. 2, figs 1–13.
 1974 *Sutneria* (*Sutneria*) *platynota* (Reinecke); Nitzopoulos, p. 81, pl. 9, fig. 14.
 1975 *Sutneria*; Ziegler, pl. 5, fig. 1.
 1977 *Sutneria platynota* (Reinecke); Ziegler, p. 21, pl. 3, fig. 3.
 1978 *Sutneria platynota* (Reinecke); Olóriz, p. 371, pl. 39, fig. 2.
 1982 *Sutneria platynota* (Reinecke); Atrops and Benest, p. 952, pl. 1, figs 4–6.
 1986 *Sutneria platynota* (Reinecke); Atrops and Marques, p. 541, pl. 1, figs 4–5.
 1990 *Sutneria platynota* (Reinecke); Bennetti *et al.* p. 34, fig. 2.
 ?1990 *Sutneria* sp. juv. cf. *platynota* (Reinecke); Bennetti *et al.* p. 34, pl. 1, figs 14–15.
 1991 *Sutneria platynota* (Reinecke); Cope, p. 329, pl. 4, figs 3, 5–6.
 1992 *Sutneria platynota*; Finkel, p. 246, fig. 83.
 1993a *Sutneria platynota* (Reinecke); Olóriz and Rodríguez-Tovar, p. 93, figs 2–3.
 1993b *Sutneria platynota* (Reinecke); Olóriz and Rodríguez-Tovar, p. 160, fig. 4c.
 1993 *Sutneria platynota* (Reinecke); Rodríguez-Tovar, p. 220, pl. 6, figs 2–4.

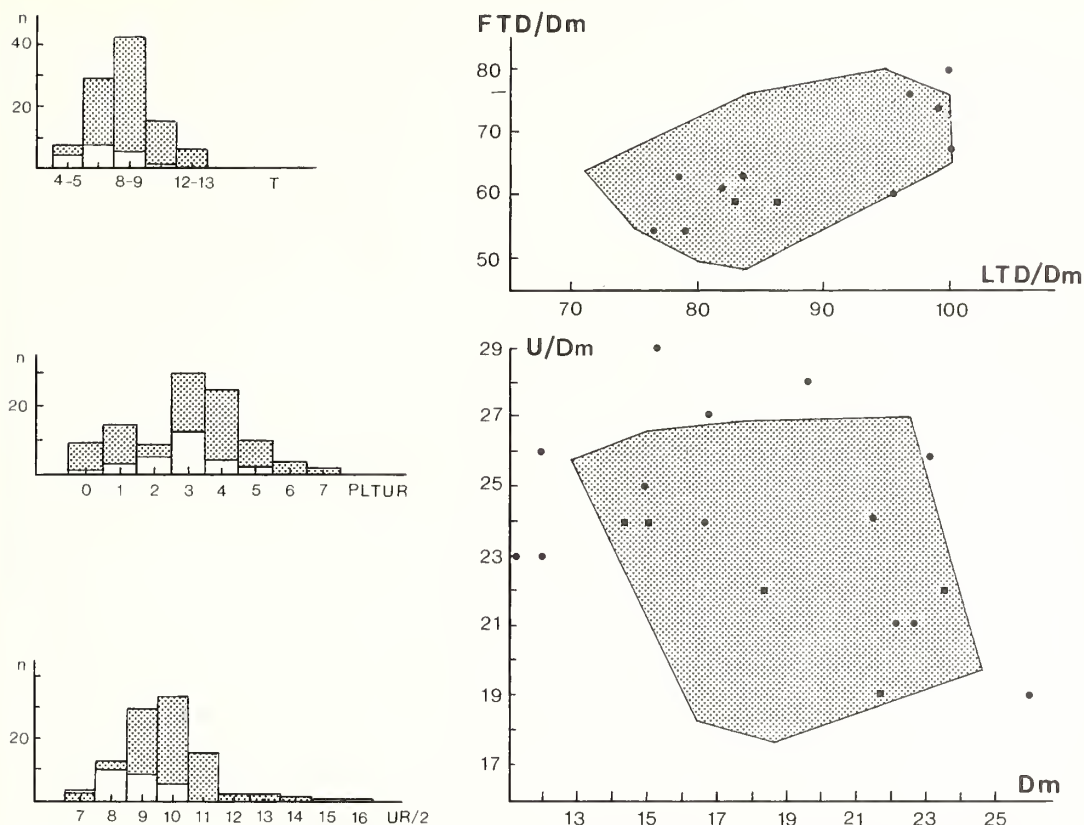
Material. Seventy-three specimens, many of which are crushed.

Dimensions.

	Dm	U	U/D	UR/2	T	FTD	LTD	PLTUR
PL-HG.C.2	16.6	4	0.24	8	8	9.9	15.8	1
PL-HG.C.3	12	3.1	0.26	10	7	9.1	11.5	1
SS-4.9	15	3.8	0.25	8	6	9.5	11.7	4
SS-6.19	11	2.5	0.23	8	7	—	10.5	≥ 2
SS-6.38	15	3.6	0.24	7	6?	≈ 12	15	—
SS-10.36	12	2.7	0.23	8–9	4	8.9	11.9	—
SS-19.A	19.7	5.5	0.28	≈ 8	5?	12.5	16.4	3
NV-0.I	23.1	5.9	0.26	—	6	15.7	23.1	0
EF-6.1	16.6	4.6	0.28	7–8	3?	—	—	2
FA-53.1	15.3	4.3	0.29	9	≥ 6	—	14.5	—
FA-75.59	18.3	4	0.22	6–7	≥ 4	—	14.6	2–3

Diagnosis. Small, involute ammonites with rounded whorls and external tubercles on the last whorl. Ribs bifurcate and polygrate with occasional ventral intercalatories. Variable pre-peristomal smoothing and whorl contraction. Pendunculate peristome.

Description. Measured specimens range from 11 to 26 mm in size. Coiling is moderately involute (19–29 per cent.). Whorl section is subrounded with broad venter. Rib density varies depending on the presence of tubercles on the last whorl. The number of umbilical ribs per half whorl is 6–10 on the outer whorl. The first appearance of external tubercles varies ($FTD/Dm = 0.54–0.76$), and the last tubercle is seen at 76–90 per cent. of the maximum diameter. The external tubercles are more or less well developed and numerous ($> 3–11$), as are the pre-peristomal primary ribs without tubercles (0–5). Five ornamental ontogenetic phases were identified: (1), on the hidden part of the phragmocone (before the last whorl), ribs range from fine to dense, and are coarse and widely spaced; division points are on the inner flanks, secondaries pass the venter without



TEXT-FIG. 4. Shell morphology of *Sutneria platynota*. Stipple represents data from southern Germany based on Schairer (1970). White areas in bars (left) and black spots (right) represent specimens from southern Spain. n = number of specimens. See text for abbreviations of shell characters.

modification and there are intercalatories; (2), rib density decreases progressively but the ribs are slightly more sinuous, divisions are higher on the flanks and secondaries are more separated; (3), primary ribs are reinforced with very small and slight radial thickening of their outer extremities to which two ventral ribs generally connect; (4), very typical strengthening of primaries which widen upwards on the flanks to connect with well-developed rounded or tangentially elongated tubercles and three ventral ribs; the progressive weakening of ventral ribs typically determines the smoothing of the venter; and (5), final developmental phase lacks external tubercles, and has a variable development of umbilical, and more or less sinuous, ribs; unsculptured shell precedes the peristome, which is pedunculate and generally with long, pointed lappets and ventral collar.

Remarks. The existence of external tubercles clearly differentiates this species from other *Sutneria*. The recognition of morphotypes ('Formengruppe'), first demonstrated by Schairer (1970) and then observed by Atrops and Benest (1982), Moliner (1983), Rodríguez-Tovar (1990) and Olóriz and Rodríguez-Tovar (1993a, 1993b) in epicontinental deposits in North Africa and Iberia, is significant but only 40 of our specimens are well enough preserved to recognize them. Incomplete preservation of the pre-peristomal part of the shell at times limited their precise identification, but we recognized seven morphotype A, nine morphotype B and three morphotype C specimens. Specimens transitional between morphotypes A and B (six) and morphotypes B and C (15) were found in both epicontinental and epiocenic (*ammonitico rosso*) facies. This must be of significance because the stratigraphical distribution of morphotypes in southern Spain is not as well differentiated as that recognized in southern Germany (Schairer 1970). In southern Spain, morphotype A specimens were recorded in the lowermost part of the sections studied, but the other morphotypes have a wide

stratigraphical distribution within the Platynota Zone. The relative abundance of Schairer's morphotypes also seems to differ from that in southern Germany. According to Schairer (1970), morphotype A and morphotype B are more abundant in the Frankischen Alb. In southern Spain, morphotype B, morphotype C and forms intermediate between them are much more common. This cannot be fully explained at present, but morphotype B and morphotype C specimens are also more common against figured specimens from other localities outside Germany. Some other differences affect shell structure and sculpture. As shown in Text-figure 4, the assemblage from southern Spain fits comfortably within the lower range in number of umbilical ribs per half whorl, number of external tubercles, and number of primary ribs after the last external tubercle as determined for southern German populations (Schairer 1970); coiling values indicate some smaller and more evolute specimens in southern Spain. On the other hand, the relative first and last appearance of external tubercles is comparable in the two regions.

Occurrence. In Europe, *Sutneria platynota* is typically found in the basal beds of the Submediterranean Kimmeridgian. According to Hantzpergue (1989), this species has not been recorded in Normandy, and is unknown in England. It is rare in Africa, with scarce records from western Algeria (Atrops and Benest 1982, 1984) and no records from the Moroccan internal Prerif (Benzaggagh 1988) and eastern Africa (Zeiss 1979, 1984). The record of six specimens of the species in northern Anatolia (Aktas Bünüs, e.g. Cope 1991) is noteworthy. Marques (1983) found rare specimens in the Algarve (southern Portugal), a record comparable to that of the nearby Betic Cordillera (Rodríguez-Tovar 1993; Olóriz *et al.* 1994). On the basis of our collection, a moderate frequency of occurrence must be considered for this species in the epicontinental Kimmeridgian in southern Spain. In the Mediterranean epiocenic Subbetic, *S. platynota* is less common, and very rare further east in the same facies (western Lessinian Alps, e.g. Benetti *et al.* 1990). Outside the Mediterranean Tethys, Burckhardt (1930) cited *S. aff. platynota* from the Barranca del río Vinasco in the Huasteca (east Mexico), but it was not figured and never collected again. During research in progress, one of us (F. Olóriz) failed to find the species in the Mexican Altiplano, or in the Burckhardt type section in the Huasteca (Veracruz, Mexico).

Sutneria galar (Oppel, 1863)

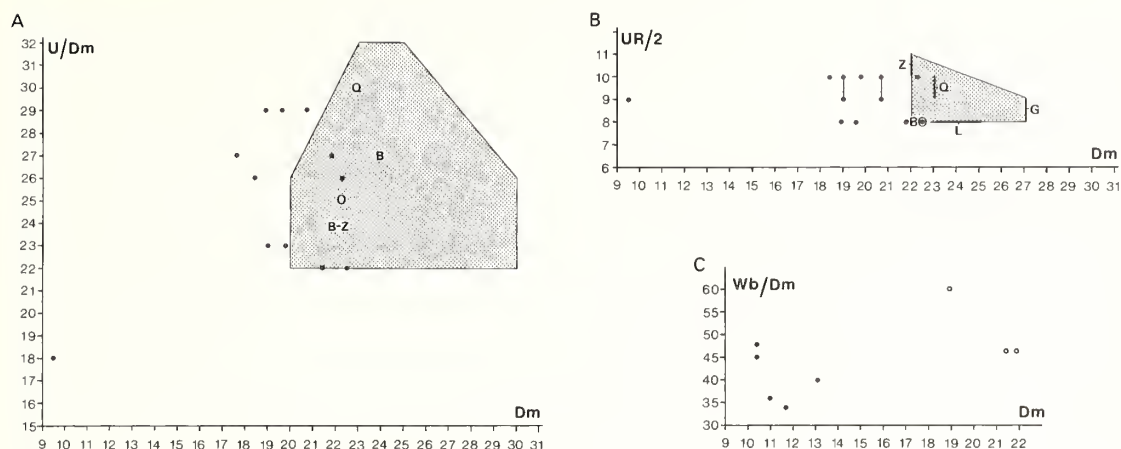
Plate 1, figures 21–29; Text-figures 5, 6A–E

- 1863 *Ammonites galar* Oppel, p. 234, pl. 67, fig. 5.
- 1878 *Ammonites (Perisphinctes) galar*, Oppel; de Loriol, p. 90, pl. 15, fig. 5.
- 1879 *Perisphinctes galar*, Oppel; Fontannes, p. 75, pl. 11, fig. 5.
- ?1887–88 *Ammonites reimeckianus* Quenstedt, p. 1002, pl. 112, fig. 17.
- 1959 *Sutneria galar* (Oppel); Barthel, p. 59, pl. 6, figs 8–10.
- 1961 *Sutneria (Sutneria) galar* (Oppel); Geyer (*partim*), p. 132, pl. 4, fig. 7.
- 1964 *Sutneria galar* (Opp.); Hölder, p. 242, fig. 73–2.
- 1969 *Sutneria galar* (Opp.); Barbulescu, pl. 2, figs 1–10.
- 1969 *Sutneria galar* (Oppel); Geyer, p. 65, fig. 1.
- 1977 *Sutneria galar* (Oppel); Ziegler, p. 19, pl. 2, fig. 3.

Material. Fifty-four specimens, commonly crushed except in condensed limestones.

Dimensions.

	Dm	U	U/D	UR/2	VR/2	RI	Wb	Wb/D
PL-Oxf.C.1	18.9	5.5	0.29	8	26	30	11.4	0.6
PL-HG.C.100	21.8	5.8	0.27	8?	≈ 28	—	10	0.46
FA-Oxf	9.5	1.7	0.18	9	22?	—	—	—
FA-4.19	22.5	5	0.22	8	27	33	—	—
FA-4.200	19.8	4.5	0.23	≈ 10	≈ 30	≈ 30	—	—
FA-4.201	20.7	5.9	0.29	9–10	31	≈ 28	—	—
FA-4.202	22.3	5.7	0.26	≈ 10	≈ 32	≈ 32	—	—
FA-4.203	17.6	4.8	0.27	—	—	—	—	—
FA-4.219	18.4	4.7	0.26	10	29	29	—	—
FA-4.229	19	4.3	0.23	9–10	> 26	> 26	—	—
FA-4.237	19.6	5.7	0.29	8	27	32	—	—
FLU ₁ .G (30–35).1	21.4	4.8	0.22	—	—	—	9.9	0.46



TEXT-FIG. 5. Shell morphology of *Sutneria galar* (Oppel) and *S. g. thieli* Zeiss. See text for abbreviations of shell characters. Black spots/circles represent Spanish specimens. A–B, stippled area represents populations from southern Germany and northern Switzerland. Data for *Sutneria galar* (Oppel) based on de Loriol (1878) and Geyer (1961); letters B, L, G, O, Q, and Z represent specimens figured respectively by Barthel (1959), de Loriol (1878), Geyer (1961), Oppel (1863), Quenstedt (1887–88) and Ziegler (1977). C, black circles represent *S. galar* (Oppel); black spots represent *S. g. thieli* Zeiss.

Diagnosis. Small and relatively involute ammonites with subrounded whorl section and broad venter. Bifurcate, polygyrate-fasciculate and intercalatory ribs on last whorl. Reduced pre-peristomal smoothing and whorl contraction. Pedunculate peristome.

Description. In the best-preserved 12 specimens, of 20 measured, size ranged from 9.5 to 22.5 mm. Coiling is moderately involute (18–29 per cent). The outer whorl is sometimes irregularly, rather than concentrically, coiled. Whorl thickness, measurable in only three specimens, is 46–60 per cent. Ribbing density fluctuates especially on the phragmocone, where ribs are mainly bifurcate with some intercalatories, but clearly decreases on the last half whorl. Towards the end of the phragmocone and on the body chamber, umbilical ribs become progressively stronger, and polygyrates and/or intercalatories increase in number. The ribs divide around mid-flank or just below. Primary ribs are slightly sinuous towards the end of the shell or before, if polygyrate ribbing appears early and is well-developed. In the latter case, more falcoid ribbing appears. Rib division very low on the flank was found near the end of the body chamber only in the smallest (?juvenile) specimen. Amongst our specimens, two morphologies were identified according to rib density and coarseness. Pre-peristomal smoothing affects first the ventral and then the primary ribs; the unsculptured shell is only 20–25 per cent. of the last whorl. The shell is less contracted at its end. Lappets are of moderate length, narrow and pointed, with a more or less distinct collar on the ventral side.

Remarks. The absence of tuberculation clearly distinguishes this species from *S. platynota*. Stratigraphical occurrence has been traditionally used to distinguish *S. galar* from other younger species such as *S. cyclodorsata* (Moesch), which is smaller, and develops more sinuous ribs and greater pre-peristomal smoothing. According to Zeiss (1979), *S. galar thieli* Zeiss is a form intermediate between *galar* and *cyclodorsata* in the lowermost Kimmeridgian. The slightly older *S. praecursor* Dieterich shows coarser, simple ribbing. This early species is rightly accepted as the ancestral form of *S. galar*. The presence of only one polygyrate rib in *S. praecursor* (recognizable on the last preserved rib in a cast of Dieterich's original; Dieterich 1940, pl. 1, fig. 2), the coarse and less densely ribbed morphotype in our own collection (similar to that figured in Quenstedt 1887–88, pl. 112, fig. 17), and the record of *Sutneria* ex gr. *galar* (Oppel) from the same horizons in the

Celtiberic range (Moscardón, Teruel, cf. Meléndez *et al.* 1983), support the hypothetical close phylogenetic relationship between *S. praecursor* and *S. galar*. Coiling values and the number of primaries per half whorl in our specimens were compared with those obtained from casts and figures of conspecific specimens mainly from southern Germany and northern Switzerland (see synonymy list above). Text-figure 5 shows comparable coiling and rib densities in the two assemblages analysed, even though the specimens from southern Spain are slightly smaller.

Occurrence. *S. galar* characterizes the uppermost Oxfordian, upper Planula Zone (Galar Subzone) in Submediterranean Europe. It has also been recorded in north-west France (Charentes, cf. Hantzpergue 1989) but not in England. In southern Submediterranean areas, like epicontinental Iberia and North Africa, *S. galar* has generally been considered to be scarce or very rare; data presented by Marques (1983, 1984), and Atrops and Marques (1986) indicate similar rarity in Portugal. Atrops and Meléndez (1984) and Meléndez *et al.* (1990) provided similar data for the north-eastern Iberian chain, but more common occurrences of *S. galar*, and/or related forms, were reported by Meléndez *et al.* (1983) from Moscardón (Teruel), a more southerly section in the Iberian Chain. In southern Spain, *S. galar*, as well as *S. praecursor*, have been identified in the Prebetic (García-Hernández *et al.* 1979, 1981; Olóriz *et al.* 1992; Olóriz and Rodríguez-Tovar 1993a, 1993b). Careful sampling in North Africa, has enabled recognition of the uppermost Oxfordian Planula Zone; specimens include *S. praecursor*, only from Algeria (Atrops and Benest 1984), but *S. galar* was not recorded. On the other hand, *S. galar* and related forms are known from epicontinental deposits in eastern Africa (Somalia, e.g. Spath 1935, and Ethiopia, e.g. Zeiss 1979, 1984). In the Mediterranean Tethys *sensu stricto*, *S. galar* has been reported locally from the Subbetic and its correlative in southern Spain (Sequeiros and Olóriz 1979; Comas *et al.* 1981), and also from Italy (Wendt 1971; Benetti *et al.* 1990), where *Sutneria* is considered to be rare (Sarti 1988). It is known rarely in Sicily (the lower occurrences of *Sutneria cyclodorsata* (Moesch) recorded by Wendt (1971)), and in Romania, *S. galar* has been recognized in the central Dobrogea (Barbulescu 1969) and in the Transylvanian nappes (Bicaz gorges-lacul Rosu area, e.g. Preda *in* Avram 1988).

Sutneria nusplingensis Fischer, 1913

Text-figure 6u

1887–88 *Ammonites reineckianus* Quenstedt, p. 1002, pl. 112, fig. 16.

1913 *Sutneria nusplingensis* n. sp. Fischer, p. 54, pl. 5, fig. 23.

Material. Only one crushed and incomplete specimen with preserved body chamber.

Diagnosis. Small ammonites with rounded whorls, moderate umbilicus and rather complex ribbing on body chamber. Pre-peristomal smoothing. No external tubercles. Pedunculate peristome.

Description. Minimum size is at least c. 23–24 mm. Primary ribs are slightly arched, prorsiradiate and clearly strengthened. Secondaries are finer, numerous (24–26 per six primary ribs) and progressively weaker towards the peristome. In the early part of the preserved body chamber, ribbing is mainly bifurcate with intercalatories, but polygyrate and/or fasciculate ribs seem to develop with increased smoothing towards the peristome, which is not preserved.

Remarks. Very rare and not well known, this is a relatively large species with uncomplicated ornament as in other early *Sutneria*. We consider the ribbing variability to be similar to that found in *S. galar* (see above). Fischer (1913) distinguished *S. nusplingensis* from *S. galar* on the basis of larger size, more regular coiling, and less contraction of the body chamber but he admitted a closer morphological relationship with the Kimmeridgian *S. cyclodorsata*, probably for stratigraphical reasons. If our interpretation is correct, *S. nusplingensis* would include relatively large *Sutneria* of the *galar*–*cyclodorsata* type, which occur rarely in the lowermost Kimmeridgian.

Occurrence. *S. nusplingensis* is known in the Lower Kimmeridgian (Platynota Zone) of southern Spain, southern Germany and northern Switzerland but it has rarely been cited since 1913, when Fischer described one specimen from the 'Weiss-Jura γ ' at Nusplingen (Swabian Alb). Geyer (1961) considered *S. nusplingensis* to be synonymous with *S. galar*, and the same as the specimen of *Ammonites reineckianus* figured by Quenstedt

(1887–88, pl. 112, fig. 16), which came from the same area and was the same age as Fischer's material. The range of *S. galar* should therefore extend up into the lowermost Kimmeridgian (lowermost part of the 'Badenerschichten' in the 'Aargauer Jura' of northern Switzerland, cf. Geyer 1961, pp. 132, 140), although the latter author restricted it to the uppermost Oxfordian in southern Germany (cf. Geyer 1961, p. 135). It is significant that *Sutneria* without external tubercles occurs in the Platynota Zone of both southern Germany and southern Spain. As recorded in the Fuente Alamo section, *S. nusplingensis* is found in the lowermost Kimmeridgian of the epicontinental deposits of the eastern Prebetic. Research in progress appears to indicate the presence of this species in western epicontinental areas of southern Iberia (Algarve, Portugal).

Sutneria galar thieli Zeiss, 1979

Text-figures 5, 6F–T

1979 *Sutneria galar thieli* n. subsp. Zeiss, p. 274, pl. 3, fig. 21.

Material. Sixteen almost complete specimens, 14 of which show the body chamber. Crushing is usual except for those specimens collected from nodular limestones.

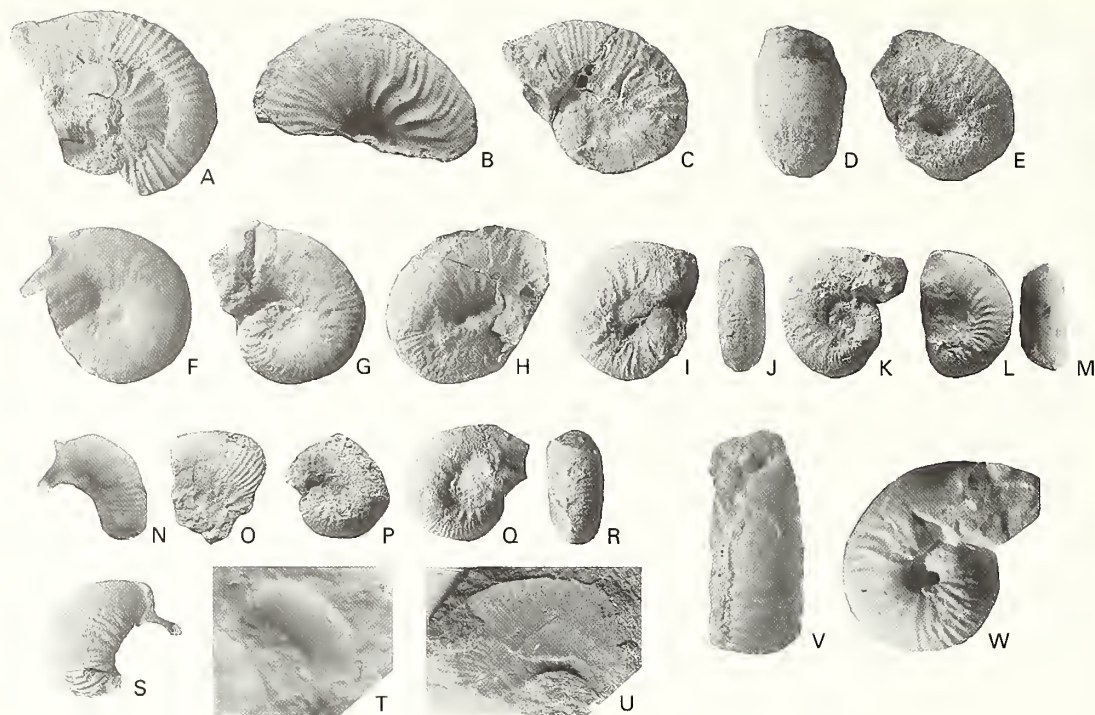
Dimensions.

	Dm	U	U/D	UR/2	VR/2	RI	Wb	Wb/D
PL-HG.C.103	10.7	3	0.28	9	≈ 22	—	—	—
	9.2	2.5	0.27	8–9	—	—	—	—
PL-Oxf.A-1	10.4	2.8	0.27	9	≈ 30	3.4	4.7	0.45
SPN ₁ .27.184	13.1	3.9	0.30	10	21	21	5.3	0.40
	10.9	3.2	0.29	≈ 11	29	26	—	—
SPN ₁ .24.120	11	2.9	0.26	15	—	18	4	0.36
	9.2	2.7	0.29	—	—	—	—	—
Z.G ₅ .5b	11.7	3.7	0.32	—	—	—	4	0.34
ZGR.47	10.4	2.4	0.23	10	24	—	5	0.48

Diagnosis. Small ammonites with subrounded–suboval whorls, moderate umbilicus, and bifurcate–polygyrate ribs. Pre-peristomal smoothing and pedunculate peristome.

Description. Sizes range from 10.4 to 13.6 mm. Coiling is moderate (23–32 per cent.), and the whorl section is subrounded or slightly oval, with a more or less broad venter. Periumbilical ribs are more or less strengthened on the body chamber, but generally indistinguishable from secondaries on the phragmocone. Ribs divide around the middle of the flanks or slightly below. Bifurcate ribs with intercalatories are dominant on the outer whorl, and polygyrates may also occur. The sinuosity of ribs and rib density is variable with UR/2 usually around 9–11, and extreme values of 7–15 on the outer whorl. Pre-peristomal smoothing first affects the peripheral sculpture and then progresses to the inner flanks. There is a slight contraction of the anterior body chamber. Thirteen specimens show the peristome, with sword-shaped ('schwertförmige') lappets, or pre-peristomal constriction and small ventral collar.

Remarks. Zeiss (1979) described *S. galar thieli* as a comparatively small subspecies found in the Lower Kimmeridgian (Platynota Zone), with variable ribbing including extreme morphologies resembling the species *subeunela*, *cyclodorsata* and *hoelderi*. He believed that it proved the phylogenetic connection between *S. galar* and that group of species. Unfortunately, the specimens studied by Zeiss are crushed, but analysis of casts of the holotype and one of the two paratypes confirms that a smaller whorl-thickness compared with *S. galar* must be added to the differences correctly stated by Zeiss. With this qualification, the specimens studied from southern Spain fit well within the morphological spectrum of *S. galar thieli* (Text-fig. 5). Compared with the known specimens from southern Germany, populations from southern Spain include smaller forms and generally show more evolute shells, with comparable rib densities only for primaries; secondaries are less numerous. Size and whorl thickness separate this species from *S. galar* and *S. nusplingensis*. The younger *S. cyclodorsata* has a comparatively globose shell. Other Oxfordian–Kimmeridgian *Sutneria* have coarser and/or more distinct sculpture.



TEXT-FIG. 6. A-E, *Sutneria galar* (Oppel, 1863); microconchs; Planula Zone (Galar Subzone). A, FA-4.219; Fuente Alamo; Bed 4. B, FA-4.200; Fuente Alamo; Bed 4. C, FA-4.207; Fuente Alamo; Bed 4. D-E, PL-HG.C.101; Puerto Lorente; ferruginized surface beneath alternating marls, marly limestones and limestones. F-T, *Sutneria galar thieli* Zeiss (1979); microconchs. F, Slg.Erl.M1; holotype (cast); Drügendorf/Ofr; Platynota Zone. G, Slg.Erl.M3; paratype (cast); Ebermannstadt/Ofr; Platynota Zone. H, FA-10.71; Fuente Alamo; Bed 10, Platynota Zone. I-J, SPN₁-27.184; Navalperal; Bed 27; Planula Zone (Galar Subzone). K, Z.G₃.5b; Sierra Gorda-Alcaudique; upper part of Bed 5; Planula Zone (Galar Subzone). L-M, SPN₁-24.120; Navalperal; Bed 24; Planula Zone (Galar Subzone). N, NV-21A.19; Navalperal; Bed 21A; Platynota Zone. O, FA-506.50; Fuente Alamo; Bed 506; Platynota Zone. P, SPN₁-27.185; Navalperal; Bed 27; Planula Zone (Galar Subzone). Q-R, PL-HG.A.1; Puerto Lorente; ferruginized surface beneath alternating marls, marly limestones and limestones; Planula Zone (Galar Subzone). S, FA-6.94; Fuente Alamo; Bed 6; Platynota Zone. T, PL-8t.53; Puerto Lorente; upper part of Bed 8; Platynota Zone. U, *Sutneria nusplingensis* Fischer (1913); FA-6.35; microconch; Fuente Alamo; Bed 6; Platynota Zone. V-W, *Sutneria praecursor*; original (cast) figured by Dieterich (1940, pl. 2, fig. 1); microconch; Nusplingen/Württemberg; 'Weisser Jura β'. Bed numbers follow Olóriz (1978) and Rodríguez-Tovar (1993). All $\times 1.5$.

Occurrence. According to present data, this species ranges from the uppermost Oxfordian (upper Planula Zone) to the lowermost Kimmeridgian (Platynota Zone) in southern Spain. In southern Germany, it has been recorded only in the Platynota Zone.

REMARKS ON THE SIGNIFICANCE OF THE AMMONITES STUDIED

Previous studies considered *Sutneria* to be a typical component of ammonite assemblages of epicontinental seas surrounding the Tethys (Ziegler 1958). This is especially true during the latest Oxfordian and Early Kimmeridgian. Rare incursions into the Subboreal realm were first interpreted as facies-controlled and related to limestone intercalations (Callomon *et al.* 1971), but later research proved otherwise (Birkelund *et al.* 1983). Recent research has provided similar evidence from other siliciclastic basins, such as northern central Mexico (Olóriz, unpublished) and the Lusitanian Basin

in western Portugal (Atrops and Marques 1986). It seems, therefore, that other factors, less directly related to depositional conditions, determined the geographical distribution of this genus.

The increasing rarity of southern records of *Sutneria* has been widely acknowledged and, when records are compared, there are stratigraphical differences between the acme of *Sutneria platynota* in southern Germany and that in south-eastern France (Ziegler 1981). Ecostratigraphical processes, at present poorly understood, could be envisaged to explain this, but the relative impoverishment in the southern records of *Sutneria* could be related also to other geological factors affecting Tethyan and southern peri-Tethyan areas, at least during the latest Oxfordian and the earliest Kimmeridgian.

Comparison of *Sutneria* records in epicontinental (Prebetic) vs epiocceanic (Subbetic) deposits in southern Spain shows a marked difference. Both *S. galar* and *S. platynota* are more common in epicontinental deposits, but stratigraphical condensation and preservation in the Subbetic *ammonitico rosso* facies could seriously affect comparative analyses. These epicontinental successions of alternating limestones and marls can be over three hundred to four hundred times thicker than the bio-chronostratigraphical equivalent in the nodular limestones, such as Subbetic *ammonitico rosso* and related facies, deposited on distal pelagic swells.

Analysis of the epicontinental deposits enables the recognition of a tectonic pulse with erosional events on the South Iberian margin around the Oxfordian-Kimmeridgian boundary (Rodríguez-Tovar 1993). Marques *et al.* (1991) called this the 'final Oxfordian crisis', to which the significant increase in subsidence in epicontinental areas during the early Kimmeridgian can be related, as can reworking phenomena affecting the uppermost Oxfordian and lowermost Kimmeridgian in distal epiocceanic areas with condensed sedimentation. In this context, it is significant that the relative biostratigraphical ranges of *S. galar* and *S. platynota* in the Prebetic and Subbetic remain unaffected except in extremely condensed and/or reworked deposits. This suggests that not only ecological factors determined the record of these species in these southern areas, as traditionally interpreted, but that other geological factors could have had a considerable influence.

In the Tethys, east of southern Spain, stratigraphical condensation and the discontinuous ammonite record must be largely responsible for the 'extreme scarcity of *Sutneria platynota* in northern Italy' described by Sarti (1988). This was confirmed by Cecca and Santantonio (1988) in the central Apennines, and previously by Wendt (1971) in Sicily. The record of rare *S. platynota* from a neptunian dyke in the western Lessinian Alps near Sant'Anna d'Alfaedo (Benetti *et al.* 1990) is consistent with our ideas. A similar context can be inferred for Romania (see Barbulescu 1969; Avram 1988), where the uppermost Oxfordian is recognized only locally in nodular limestones with *S. galar* (Preda 1973 in Avram 1988). In North Anatolia, *S. platynota* (Reinecke) has also been found in condensed deposits (Cope 1991).

As we commented above, records of *Sutneria* from around the Oxfordian-Kimmeridgian boundary in North Africa are also scarce. Sedimentation was clearly affected by important increases in siliciclastics and even emersions at that time, and discontinuity in the ammonite record is well known (Atrops and Benest 1992). In this case, it is significant that in the younger horizons containing *S. platynota*, the species is represented by the younger morphotype C of Schairer (1970) (cf. Atrops and Benest 1982).

Increased siliciclastics, sampling difficulties and probable stratigraphical discontinuities prevent precise control of the *Sutneria* record around the Oxfordian-Kimmeridgian boundary in the classic Montejunto region (western Portugal), as deduced by Atrops and Marques (1986). This is also the case in the Iberian Chain, as can be seen in the overview by Meléndez *et al.* (1990).

In this context, the record of 144 *Sutneria* specimens collected bed-by-bed around the Oxfordian-Kimmeridgian boundary on the South Iberian margin represents a valuable source of information on the best known southern assemblage of this genus. Data obtained for the upper Planula Zone (uppermost Oxfordian) and the Platynota Zone (lowermost Kimmeridgian) enables us to: (1), form a more exact idea of the distribution of *Sutneria* in southern areas related to the Tethys during this interval; (2), undertake an initial evaluation of the differences between these southern populations and the previously better known populations from southern Germany and northern Switzerland; and (3), recognize the role of the geological factors that prevented the straightforward, traditional

interpretation of the *Sutneria* record, particularly in epioceanic areas, on the basis of strictly palaeobiological and palaeoecological considerations.

From a biostratigraphical viewpoint, the following appear to be well established and/or significant facts: (1), strongly sculptured specimens of *Sutneria platynota* ('Formengruppe' A of Schairer (1970)) are restricted to the basal part of the Kimmeridgian, even in condensed limestones; (2), other morphotypes of *S. platynota* ('Formengruppe' B and C of Schairer (1970)) have a wider distribution, generally including the complete stratigraphical range of this species in the study area; (3), the rare *S. nusplingensis* is found at the very base of the Platynota Zone; (4), *S. galar thieli* ranges from the upper Planula Zone to the Platynota Zone; and (5), there is no bed with identified ammonites between the last recorded occurrence of *S. galar* and the first appearance of *S. platynota*.

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THE HIRNANTIAN GRAPTOLITES *NORMALOGRAPTUS PERSCULPTUS* AND '*GLYPTOGRAPTUS*' *BOHEMICUS*: STRATIGRAPHICAL CONSEQUENCES OF THEIR SYNONYMY

by PETR ŠTORCH and DAVID K. LOYDELL

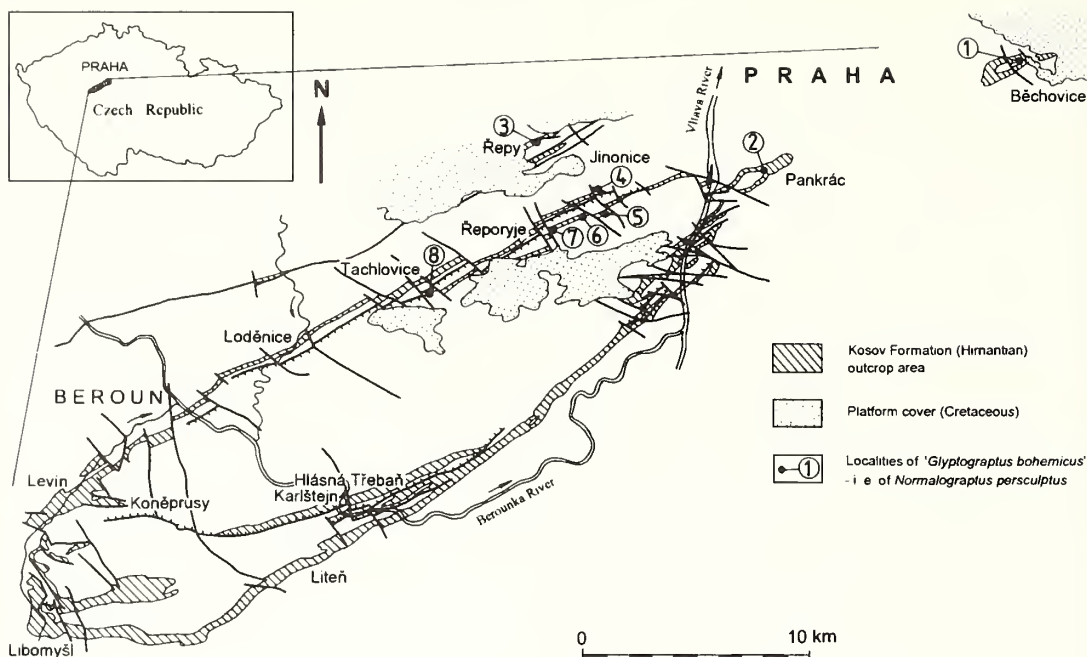
ABSTRACT. It is demonstrated that '*Glyptograptus*' *bohemicus* is a junior subjective synonym of *Normalograptus persculptus*. The first appearance of *N. persculptus* appears to be diachronous, posing problems for Hirnantian biozonation. In China, *N. persculptus* co-occurs with *N. extraordinarius*. We favour here an extension downwards of the existing *persculptus* Biozone, the base being defined by the incoming of *N. persculptus*, with the lower part of the biozone designated the *extraordinarius* Subzone.

THERE has not been agreement among graptolite workers as to the taxonomic and stratigraphical relations between *Normalograptus persculptus* (Elles and Wood, 1907) and '*Glyptograptus*' *bohemicus* Marek, 1955. Many authors (e.g. Štorch 1982, 1988; Wang *et al.* 1983; Chen and Lin 1984; Li 1984; Mu and Lin 1984; Ni 1984; Fu and Song 1986; Wang 1987; Mu 1988; Fang *et al.* 1990; Melchin *et al.* 1991) considered the two taxa to be distinct and used them as index species for two separate biozones within the Hirnantian Stage (Ashgill Series, Ordovician). Below the *persculptus* Biozone, which is recognized globally, a *bohemicus* Biozone has been introduced in the graptolite biozonal schemes of Bohemia, China and Arctic Canada. Other authors (Koren' and Sobolevskaya 1983; VandenBerg *et al.* 1984; Štorch 1994), however, have considered *N. persculptus* and '*G.*' *bohemicus* to be synonyms. Herein we redescribe the type and all other available Bohemian specimens of '*G.*' *bohemicus* and compare them with Welsh material of *N. persculptus*. Brief comparison with selected Chinese material is also included. We demonstrate that '*G.*' *bohemicus* is a junior subjective synonym of *N. persculptus* and discuss the stratigraphical consequences of this synonymy.

STRATIGRAPHICAL FRAMEWORK FOR THE BOHEMIAN MATERIAL

All the Bohemian specimens of '*G.*' *bohemicus* come from the uppermost beds of the Kosov Formation (Text-figs 1–2). This is a glacio-eustatically controlled regressive-transgressive sequence, c. 100 m thick, of Hirnantian age. Diverse, deep-shelf Rawtheyan faunas, which characterize the clayey shales of the underlying Králův Dvůr Formation, disappear just below the base of the Kosov Formation (Štorch and Mergl 1989), and are replaced by the low-diversity *Mucronaspis* Assemblage, which occurs in Hirnantian deeper-water environments. The base of the Kosov Formation is marked by two levels of pebbly glacio-marine diamictites (Brenchley and Štorch 1989). These suggest that, in the early Hirnantian, at an early stage of regression, floating ice extended over the Prague Basin. The continuing regression is documented by the overlying, rhythmically bedded tempestites. The middle part of the Kosov Formation is suggestive of a temporary sea-level rise, being composed of a shaly sequence with few thin siltstone intercalations.

The upper part of the Kosov Formation is represented by another rhythmically bedded tempestite unit. This has, above its sharp erosional base, several thick beds of coarse sandstones and

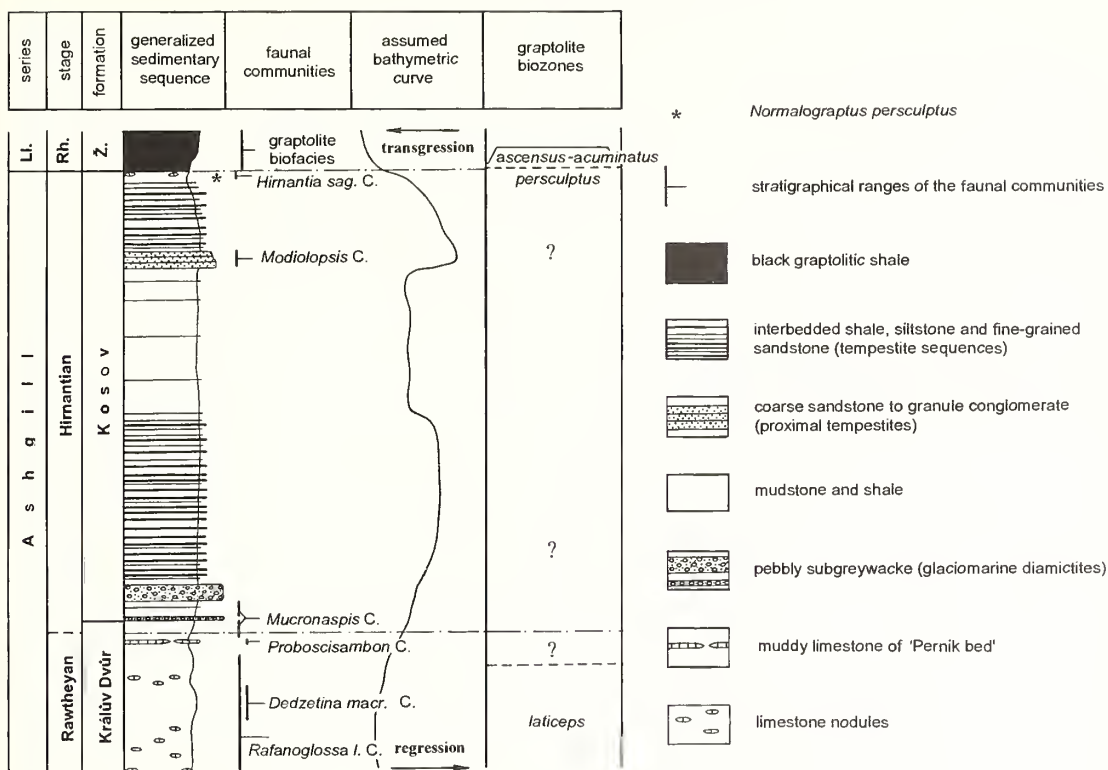


TEXT-FIG. 1. Localities where *Normalograptus persculptus* (formerly '*Glyptograptus*' *bohemicus*) has been found in the Barrandian area in Bohemia, with Gauss-Krueger grid references: 1 – Běchovice, X5551248, Y3457177; 2 – Pankrác, X5547359, Y3460644; 3 – Řepý, X548661, Y3450474; 4 – Nové Butovice, X5546447, Y3453087; 5 – Jinonice-Nová Ves, X5545574, Y3453632; 6 – Velká Ohrada, X5545512, Y3452675; 7 – Reporyje, X5445061, Y3451663; 8 – Tachlovice, X5547359, Y3446006.

conglomerates. According to Brenchley and Štorch (1989), these indicate a second regressive event with the shelf channelled and coarse material supplied from the shore. The sedimentary structures described by Brenchley and Štorch (1989), ichnofacies described by Mikuláš (1993), and very low diversity bivalve assemblage listed by Havlíček (1982) all come from the period of maximum glacio-eustatic regression at the base of the upper tempestite unit of the Kosov Formation. The bathymetric curve of Štorch (1990) for the Kosov Formation fits well the bathymetric changes suggested by, for example, Brenchley (1984) and Brenchley *et al.* (1991). The remainder of the upper, rhythmically bedded tempestite unit was deposited during a transgression which accelerated towards the top of the Kosov Formation.

The uppermost part of the Kosov Formation was deposited under deeper-subtidal conditions, well below storm-wave base. In the north-east part of the Barrandian area it is composed of heavily bioturbated mudstones, with a varied, brachiopod-dominated *Hirnantia* Fauna (Marek and Havlíček 1967; Štorch 1986) and '*G.*' *bohemicus*. This fauna has been recorded at Běchovice, Jinonice-Nová Ves, Nové Butovice, Pankrác, Řepý, Tachlovice (borehole) and Velká Ohrada (Text-fig. 1).

Both the *Hirnantia* Fauna and the graptolite rhabdosomes are confined to this rather thin (50 mm–4.5 m thick) horizon. The highest identifiable '*G.*' *bohemicus*, found together with uncommon brachiopods, were about 70 mm below the base of the overlying black Silurian shales, which yield *Normalograptus angustus* (Perner), *Akidograptus ascensus* Davies and *Neodiplograptus lanceolatus* Štorch and Serpagli. At some localities described by Štorch (1986; Řepý, Vočkov and Želkovic) 20–30 mm of black and white, laminated shale forms the transition from the pale mudstones to the Silurian black shales, without any apparent gap in sedimentation. This



TEXT-FIG. 2. The upper Ashgill stratigraphy of the Barrandian area, Bohemia, showing the stratigraphical level of Bohemian specimens of *Normalograptus persculptus* (formerly '*Glyptograptus bohemicus*'). The thickness of the Kosov Formation varies between 40 and 150 m. Abbreviations: C. – community; Li. – Llandovery; Rh. – Rhuddanian; Ž. – Želkovice Formation. Not drawn to scale.

transitional bed, still below the first appearance of *A. ascensus*, contains poorly preserved normalograptids, including the specimens referred by Štorch (1982, 1986) to '*G. bohemicus-persculptus*'.

The *Hirnantia* Fauna and '*G.*' *bohemicus* have been recorded in the Barrandian area at the same level from which *Normalograptus persculptus* and associated graptolites are reported elsewhere. Although the two species could be regarded as coeval, palaeogeographically restricted subspecies, because of their identical dimensions and morphology, we prefer to consider '*G.*' *bohemicus* to be a junior subjective synonym of *N. persculptus* (Elles and Wood).

Institutional abbreviations are: GSM, British Geological Survey, Keyworth, Nottingham; L, National Museum, Prague; PŠ, Štorch collection, Czech Geological Survey, Prague.

SYSTEMATIC PALAEOONTOLOGY

Family NORMALOGRAPTIDAE Štorch and Serpagli, 1993

Genus NORMALOGRAPTUS Legrand, 1987

Type species. By original designation, *Climacograptus scalaris normalis* Lapworth, 1877, from the Birkhill Shales, Dob's Linn, Scotland.

Diagnosis (modified from Melchin and Mitchell 1991). Rhabdosome suboval to nearly circular in cross section. Median septum straight or slightly wavy in the proximal part, usually complete. Early astogeny of Pattern H, with th2 or, rarely, some later theca dicalycal. Proximal end relatively narrow, rounded, asymmetrical. Climacograptid to almost glyptograptid thecae have angular or sigmoidal genicular curvature.

Remarks. The original conception of the genus, reflected in the diagnoses given by Legrand (1987) and Štorch and Serpagli (1993), has been extended to embrace the late Ordovician and early Silurian glyptograptid-like species with Pattern H astogeny.

Normalograptus persculptus (Elles and Wood, 1907)

Text-figures 3–5

- 1865 *Diplograptus persculptus* (Salter?), Salter, p. 25 [see Strachan 1971].
- 1907 *Diplograptus* (*Glyptograptus*) *persculptus* Salter; Elles and Wood, p. 257, pl. 31, fig. 7a–c; text-fig. 176a–b.
- 1929 *Glyptograptus* aff. *persculptus* Salter; Davies, p. 10, text-fig. 11A.
- 1929 *Glyptograptus persculptus* mut.; Davies (*pars*), p. 11, text-figs 11, 13, 16–19 (*non* 12, 14).
- 1929 *Glyptograptus persculptus* mut. *omega* nov., Davies, text-figs 15, 20.
- 1955 *Glyptograptus bohemicus* Marek, p. 7, pl. 1, figs 1–4.
- 1971 *Glyptograptus* (*G.*) *persculptus persculptus* (Salter); Strachan, p. 37.
- 1973 *Glyptograptus persculptus* (Salter); Mikhaylova, p. 15, pl. 3, figs 4–6.
- non* 1974 *Glyptograptus persculptus* (Salter); Hutt, p. 28, pl. 8, figs 9–12.
- 1975 *Glyptograptus persculptus* (Salter); Bjerreskov, p. 30, text-fig. 11a–c.
- 1977 *Glyptograptus bohemicus* Marek; Jaeger, pl. 1, figs 4, 6, 9, 11, 17.
- 1977 *Glyptograptus* aff. *bohemicus* Marek; Koren' and Sobolevskaya, figs 5–7.
- 1977 *Glyptograptus persculptus* (Salter); Rickards *et al.*, pl. 2, fig. 4, text-figs 8, 53
- 1978 *Glyptograptus persculptus* (Salter); Sennikov, p. 142, text-fig. 3i, k.
- 1980 *Glyptograptus?* *persculptus* (Salter); Koren' *et al.*, pl. 43, figs 2–3.
- 1980 *Glyptograptus?* *persculptus* (Salter) forma B; Koren' *et al.*, p. 150, pl. 45, figs 1–6; pl. 46, figs 1–6 (?7–8); text-fig. 45a–zh.
- 1982 *Glyptograptus bohemicus* Marek; Štorch, pl. 2, figs 5–6.
- 1983 *Glyptograptus persculptus* Salter; Koren' and Sobolevskaya, p. 144, pl. 42, figs 4–10; pl. 43; text-fig. 54 (*pars*).
- 1983 *Diplograptus bohemicus* (Marek); Mu *et al.* (*pars*), pl. 2, figs 3, 10 (*non* 4).
- 1983 *Glyptograptus persculptus* (Salter); Wang *et al.*, p. 139, pl. 8, figs 3–6; pl. 9, figs 5, 10–11.
- 1983 *Diplograptus bohemicus* (Marek); Wang *et al.*, pl. 7, figs 1–3, ?11.
- 1983 *Glyptograptus persculptus* (Salter); Williams, p. 622, pl. 66, figs 1–3.
- 1984 *Glyptograptus persculptus* (Salter); Chen and Lin, p. 193, pl. 1, figs 1–6; pl. 2, figs 3–9; text-fig. 1.
- 1984 *Diplograptus bohemicus* (Marek); Ge, p. 411, pl. 3, figs 10–14, ?15; text-fig. 3.
- 1984 *Diplograptus bohemicus* (Marek); Li, p. 335, pl. 8, fig. 6, ?1–5.
- 1984 *Glyptograptus persculptus* (Salter); Lin and Chen, pl. 1, figs 1–2.
- ?1984 *Glyptograptus lungmaensis* Sun; Lin and Chen (*pars*), p. 209, pl. 1, figs 3, 6 (*non* 4–5).
- ?1984 *Diplograptus bohemicus* (Marek); Mu and Lin, p. 53, pl. 3, figs 1–3.
- 1984 *Glyptograptus persculptus* (Salter); Mu and Lin, p. 54, pl. 3, fig. 6; pl. 6, fig. 9.
- 1984 *Diplograptus bohemicus* (Marek); Ni, p. 323, pl. 2, figs 6–8.
- 1984 *Glyptograptus?* *persculptus* (Salter); VandenBerg *et al.*, p. 10, figs 8–9.
- 1986 *Diplograptus bohemicus* (Marek); Fu and Song, p. 76, pl. 4, fig. 6 (?*non* 5); text-fig. 6g.
- 1986 *Glyptograptus persculptus* (Salter); Fu and Song, p. 80, pl. 4, figs 23–24, (?*non* 22).
- 1986 *Glyptograptus bohemicus* Marek; Štorch, pl. 3, fig. 8.
- ?1987 *Glyptograptus persculptus* (Salter); Wang, p. 370, pl. 45, fig. 1.
- 1987 *Diplograptus bohemicus* (Marek); Wang, p. 375, pl. 43, fig. 1.
- 1990 *Diplograptus bohemicus* (Marek); Fang *et al.*, p. 46, pl. 1, figs 11–12; pl. 2, figs 2–3; pl. 4, fig. 6.

- 1990 *Glyptograptus persculptus-sinuatus* transient; Fang *et al.*, p. 60, pl. 8, figs 2–3, 6.
 1993 *Diplograptus bohemicus* (Marek); Mu *et al.*, p. 129, pl. 21, figs 1–3, ?4–5.
 1994 *Normalograptus? persculptus* (Elles and Wood); Zalasiewicz and Tunnichiff, p. 704, fig. 5a–c.

Lectotype. Designated by Williams 1983; GSM 11782 from Salter's collection; Ogofau, Pumpsaint, Dyfed, Wales; figured Williams 1983, plate 66, figure 3.

Material. Eighteen specimens of '*Glyptograptus*' *bohemicus* (including the type material of Marek 1955) from the Barrandian area (Bohemia); most are complete, preserved flattened or in partial relief. Numerous specimens of *Normalograptus persculptus* from localities in mid-Wales, preserved flattened and in moderate to full relief. One of us (DKL) has also examined specimens from China figured by Ge (1984), Li (1984), Mu and Lin (1984) and Ni (1984). All specimens are from the Hirnantian (late Ordovician) *N. persculptus* Biozone.

Diagnosis. Rhabdosome straight, widening from 1.0 mm (0.8 mm in relief) to a maximum of 2.0–2.5 mm at a distance of 10–15 mm from the proximal end; median septum complete in early populations, slightly wavy in specimens preserved in relief. Successive delay in the insertion of the median septum appears in stratigraphically late populations. Alternate to subalternate sigmoidally curved thecae of glyptograptid appearance become strongly geniculate in flattened rhabdosomes; thecae overlap for half of their length and number 5–6 in the proximal 5 mm and 8–10 in 10 mm distally.

Description (of Bohemian material). The rhabdosome is up to 28 mm long, excluding the virgella and nema. It widens from 0.8 mm (1.1–1.3 mm when flattened) at the aperture of $th1^1$ to 1.1 mm (1.6 mm when flattened) at $th3^1$, and reaches a maximum of 1.6–1.7 mm (1.9–2.3 mm when flattened) within 8–10 mm of the proximal end. Thecae number 5.5–5.8 in the proximal 5 mm. Distally the thecal count decreases to 10–10.5 in 10 mm.

The sicula, visible for at least 1 mm in obverse view, is conical, with a c. 2 mm long virgella. The sicular aperture has a diameter of 0.2–0.25 mm. $Th1^1$ grows downwards, then, 0.15–0.25 mm below the sicular aperture, bends abruptly upwards. The distance between the sicular aperture and the aperture of $th1^1$ is 0.85–0.9 mm. $Th1^2$ grows upwards for its entire length and this gives a distinctive, asymmetrical appearance to the proximal end.

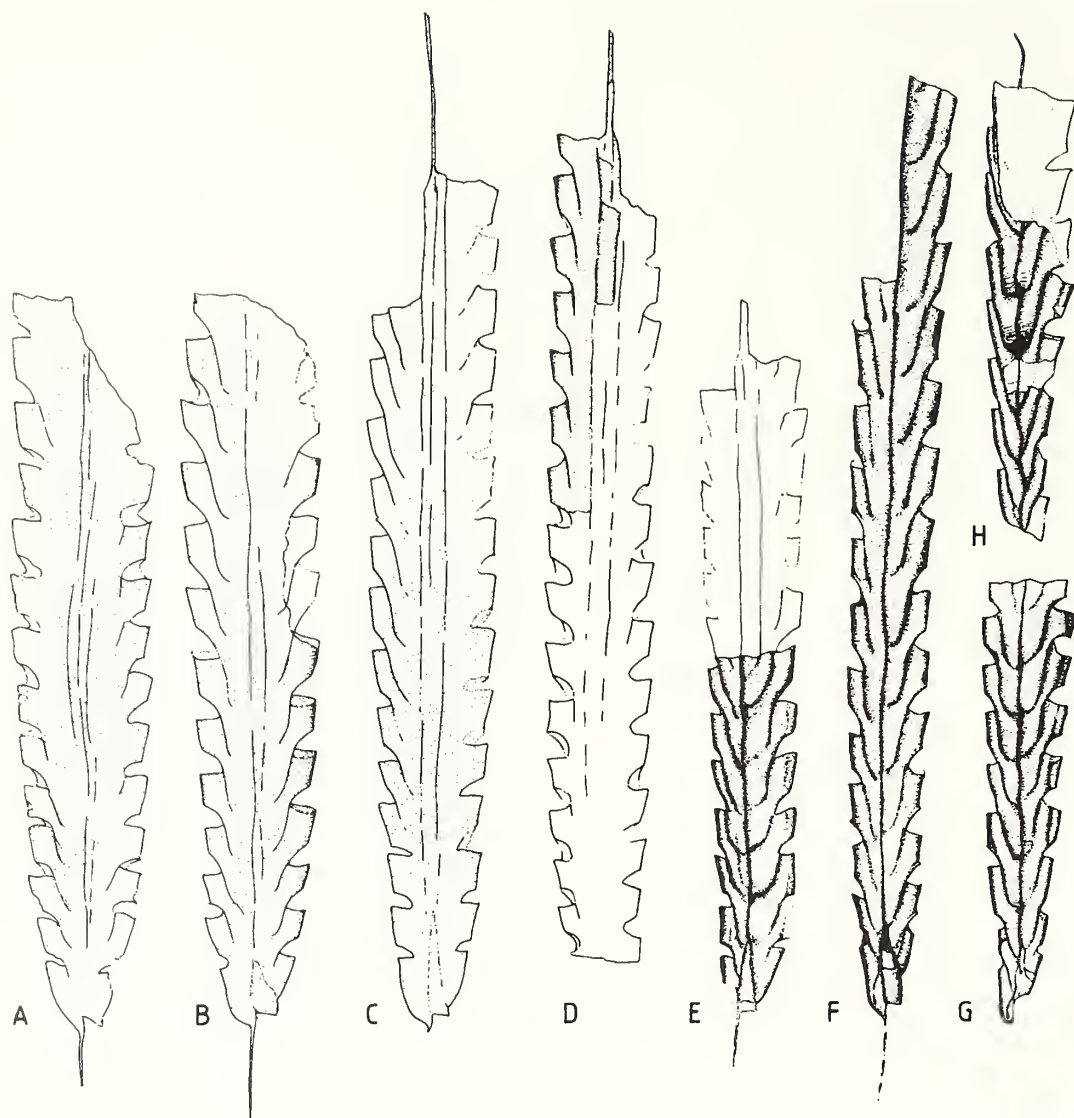
The appearance of the thecae depends upon preservation. Sigmoidally curved thecae with sharp genicula are typical of flattened (including the type) material (from the Jinonice-Nová Ves and Velká Ohrada sections; see e.g. Text-fig. 3A, c). Their supragenicular walls are straight, inclined at c. 10° to the rhabdosome axis. Specimens preserved in low relief (from Jinonice, Řepy and Pankrác) and moderate relief (from Pankrác) are of more glyptograptid appearance (Text-fig. 3F–H), but they are still strongly geniculate in some cases. Thecal apertures are straight, horizontal or slightly everted. Thecal excavations occupy c. one-fifth of the dorso-ventral width. The subalternate distal thecae are 1.5–1.8 mm long and overlap for up to half their length. Intertheal septa reach to about the level of the aperture of the preceding theca.

The median septum appears to be complete. It is slightly undulating in the proximal part of the rhabdosome. The rhabdosome commonly becomes uniserial distally. The nema is distinctly thickened at the base, probably as a result of distal prolongation of the median septum.

Specimens of *N. persculptus* from mid-Wales are illustrated in Text-figures 4D–E and 5 for comparison with the Bohemian material described above.

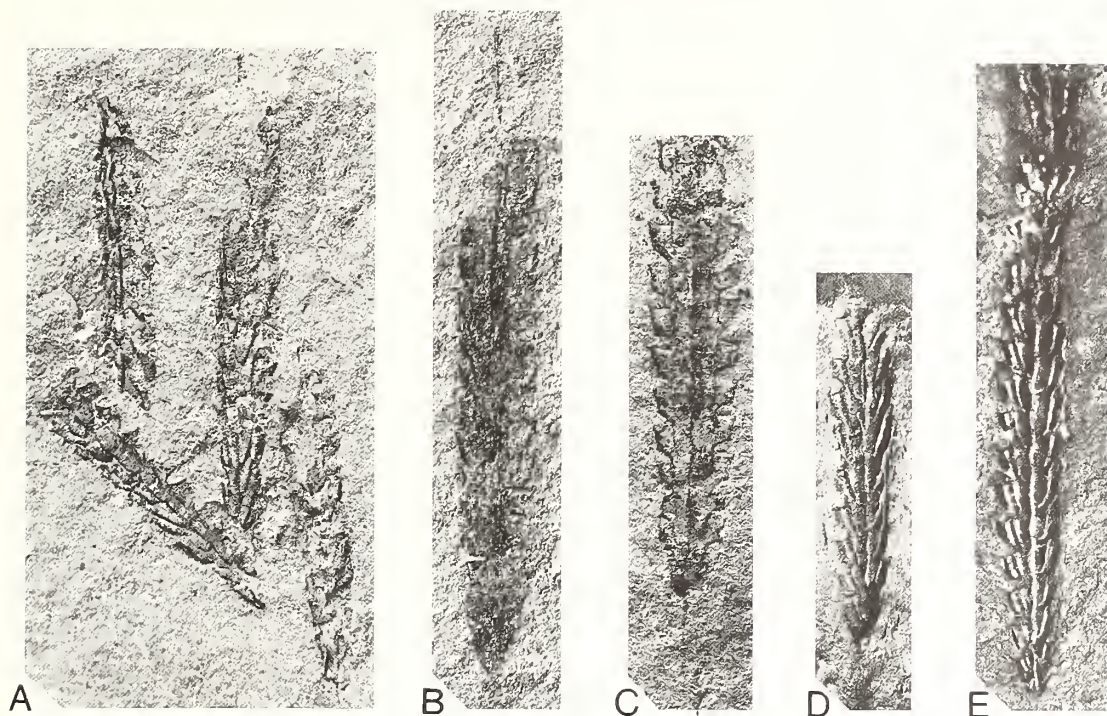
Remarks. Elles and Wood (1907) are regarded here as the authors of *N. persculptus*; Salter (1865) neither figured nor described this species (see discussion in Williams 1983 and Zalasiewicz and Tunnichiff 1994).

The Bohemian material of '*G.*' *bohemicus* agrees well with the Welsh material illustrated herein, and with the British and Scandinavian specimens of *N. persculptus* described by Williams (1983) and Bjerreskov (1975) respectively, as well as the material described by Koren' *et al.* (1980) from Kazakhstan, by Koren' and Sobolevskaya (1983) from Siberia, and by VandenBerg *et al.* (1984) from Australia (Table 1). The distal end of Bohemian rhabdosomes is, however, more commonly uniserial. This latter tendency has been illustrated by Williams (1983) in *Normalograptus venustus* (Legrand), by Lin and Chen (1984) in '*Glyptograptus*' *lungmaensis* Sun and



TEXT-FIG. 3. Bohemian specimens of *Normalograptus persculptus*. A, PŠ 648a; flattened specimen, with periderm. B, PŠ 278/2; preserved in very low relief, with periderm. C, L 14651, holotype of '*Glyptograptus*' *bohemicus*; flattened, partly limonitized film. D, PŠ 278/1; very low relief external mould with some periderm. E, L 14650; preserved in low relief, distally as an external mould. F, PŠ 130; preserved in low relief, with periderm. G-H, PŠ 662a (two rhabdosomes on one slab); preserved in low to moderate relief. Localities: A, Velká Ohrada; B-E, Jinonice-Nová Ves; F, Řepy; G-H, Pankrác. All $\times 8$.

'*Climacograptus*' *wangjiawanensis* Mu and Lin, by Ge (1984) in '*Diplograptus*' *maturatus* Mu and Ni, and commonly in the rhabdosomes referred to '*G.*' *bohemicus* in China. A specimen of *N. persculptus* with four uniserial distal thecae is present in our collections from Rhayader, Wales. The presence of a uniserial distal portion, perhaps the result of some astogenetic mutation, cannot be used as a morphological criterion for separating '*G.*' *bohemicus* from *N. persculptus*.

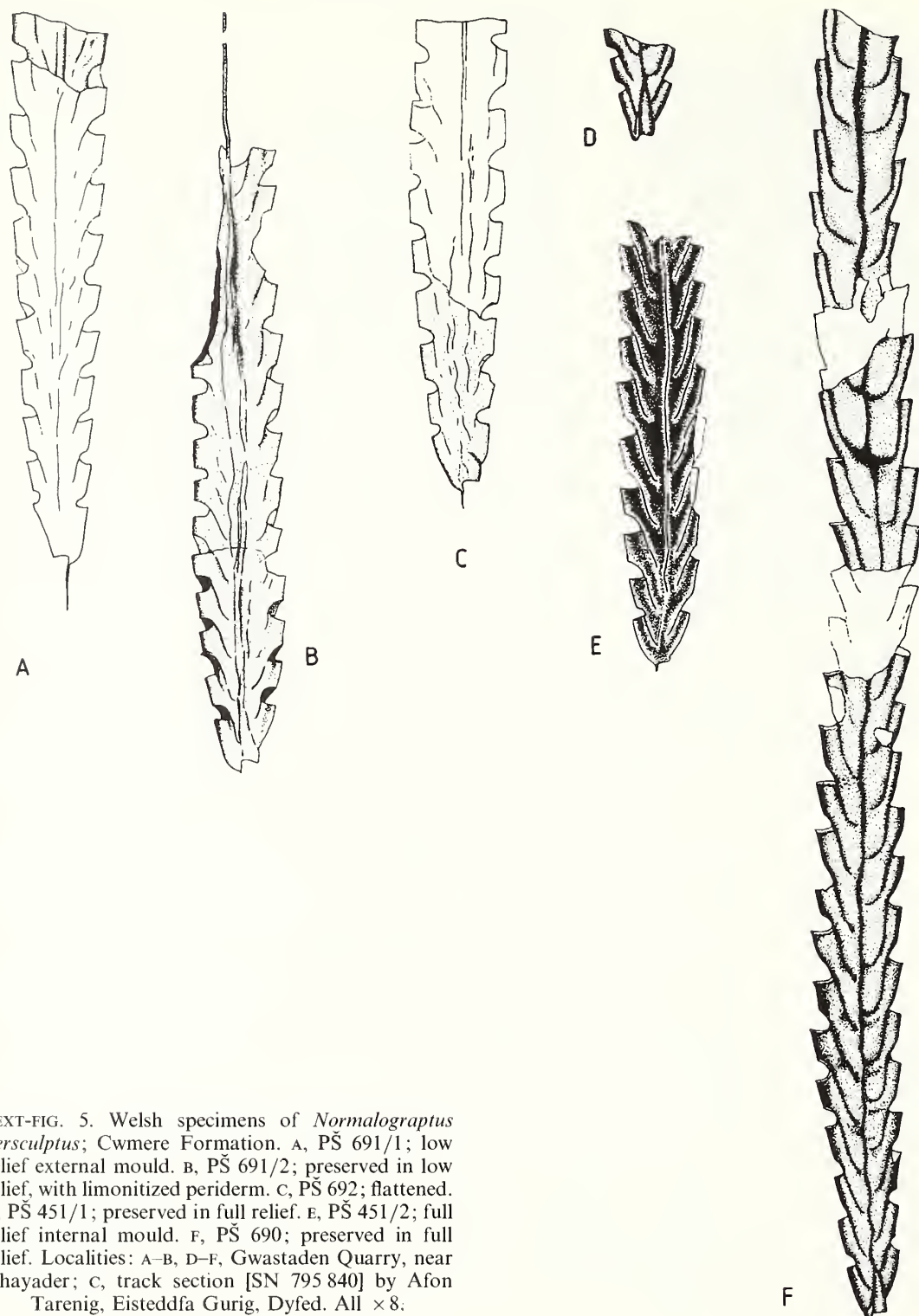


TEXT-FIG. 4. *Normalograptus persculptus* (Elles and Wood, 1907). A, PŠ 662a; four specimens preserved in low to moderate relief, with periderm. B, L 14651, holotype of '*G.*' *bohemicus*; flattened, partly limonitized film. C, PŠ 278/2; preserved in very low relief, with periderm. D, PŠ 451/2; full relief, internal mould. E, PŠ 690; full relief, internal mould. Localities: A, Pankrác, Bohemia; B–C, Jinonice-Nová Ves, Bohemia; D–E, Cwmere Formation, Gwastaden Quarry [SN 970 656], near Rhayader, Powys, Wales. All $\times 5$.

Zalasiewicz and Tunnicliff (1994) assigned Hutt's (1974) specimens from the English Lake District to *N.?* *parvulus* (H. Lapworth). This species is significantly narrower than *N. persculptus* and post-dates it stratigraphically (see Zalasiewicz and Tunnicliff 1994 for details).

HIRNANTIAN GRAPTOLITE BIOZONATION

Jaeger (1977) figured '*G.*' *bohemicus* from the uppermost part of the Dobra Sandstone in Saxony (Germany). His material came from a level which corresponds approximately with the *bohemicus*-bearing beds in Bohemia. Most reports of the species, however, are from China, where it is usually assigned to *Diplograptus*. In China a *bohemicus* Biozone is widely recognized below the *persculptus* Biozone, being regarded as a stratigraphical equivalent of the *extraordinarius* Biozone (Li *et al.* 1983; Mu *et al.* 1983; Wang *et al.* 1984; Mu 1988). The index species is accompanied by faunas including *Paraorthograptus typicus* Mu, *Climacograptus supernus* Elles and Wood and *Normalograptus extraordinarius* (Sobolevskaya). The Chinese *bohemicus* Biozone is commonly separated from the succeeding *persculptus* Biozone by beds containing a rich, shelly *Hirnantia* fauna. According to Mu (1988), these beds correspond with the time of maximum Hirnantian glacio-eustatic regression and clearly precede the post-glacial transgressive sequence of the *persculptus*



TEXT-FIG. 5. Welsh specimens of *Normalograptus persculptus*; Cwmere Formation. A, PŠ 691/1; low relief external mould. B, PŠ 691/2; preserved in low relief, with limonitized periderm. C, PŠ 692; flattened. D, PŠ 451/1; preserved in full relief. E, PŠ 451/2; full relief internal mould. F, PŠ 690; preserved in full relief. Localities: A–B, D–F, Gwastaden Quarry, near Rhayader; C, track section [SN 795 840] by Afon Tarenig, Eisteddfa Gurig, Dyfed. All $\times 8$.

TABLE 1. Measurements of dorso-ventral width, rhabdosome length, thecal count and thecal overlap in *Normalograptus persculptus*. Specimens are preserved flattened (F), in low to moderate relief (M) or full relief (R).

material, described by	preservation	width					length max.	thecal count		thecal overlap
		prox.	5th thecal pair	5 mm from prox.	10 mm from prox.	dist. max.		/ prox. 5 mm	/ dist 10 mm	
<i>persculptus</i> Elles and Wood (1907)	M-R	1.0	/	/	/	2.0-2.5	> 30	/	8-10	1/2
<i>persculptus</i> Williams (1983)	M-R	1.0	/	1.5-1.7	/	2.0-2.7	30	5.5	9	/
<i>persculptus</i> this paper (mid-Wales)	R	0.85-0.95	1.45	/	1.7-1.8	1.95	37	5-6	8.5-10	1/2
	F	0.95-1.15	1.55-1.75	/	1.8-1.95	2.2				
<i>persculptus</i> Bjerreskov (1975)	R	1.0	1.5	/	/	1.6	20	5	9.5-10	1/2
	F					2.0				
<i>persculptus</i> Koren and Sobolevskaya (1983)	F	1.05-1.25	1.7-1.8	1.85-2.0	1.9-2.2	2.25	45	5-5.5	9.5-10	1/2-1/3
<i>persculptus</i> forma B Koren et al. (1980)	M	1.0-1.1	1.5-1.7	1.6-1.75	1.75-2.0 (2.5)	2.0	35	5-6	9-10	1/2
	F					2.5				
'bohemicus' this paper (Bohemia)	M	0.8	1.45-1.6	/	1.6-1.7	2.35	28	5.5-5.8	10-10.5	1/2
	F	1.1-1.3	1.6-1.95		1.9-2.3					
'bohemicus' Mu and Lin (1984)	F	1.0-1.2	/	1.7	2.0	2.0	27	5.5	10	1/2
'bohemicus' Ge (1984)	F	1.4 (1.15-1.25)	1.6-1.7	1.8	2.2-2.3	2.3	20	5	8	1/2
'bohemicus' Li (1984)	F	1.0-1.2	/	1.8-2.0	2.1-2.2	2.2	>13	5-5.5	/	1/2-2/3
'bohemicus' Chen and Lin (1984)	F	1.0-1.2	/	2.0-2.1	2.0-2.1	2.2	27	/	10-11	1/2
<i>persculptus</i> Chen and Lin (1984)	F	1.0-1.5	/	1.5	1.7	2.1	22	/	10-11	1/2-2/3

Biozone. In Arctic Canada Melchin *et al.* (1991) found specimens of '*G.*' *bohemicus* just above beds which yielded *Paraorthograptus pacificus* (Ruedemann). The Bohemian specimens of '*G.*' *bohemicus* are almost certainly younger than those assigned to this taxon from Chinese and Canadian sequences.

Koren' and Sobolevskaya (1983) placed '*G.*' *bohemicus* into synonymy with *N. persculptus* after conducting a detailed study of the latter taxon from Siberia (Omulevka Uplift) and Kazakhstan (Koren' *et al.* 1980). Our study, primarily of Bohemian and Welsh specimens, confirms this synonymy. By contrast with the Chinese sections, where '*G.*' *bohemicus* and *N. extraordinarius* commonly occur together, in the sections described by Koren' *et al.* (1980) and Koren' and Sobolevskaya (1983) the earliest *N. persculptus* succeed the youngest specimens of *N. extraordinarius* without any overlap of their stratigraphical ranges.

With '*G.* *bohemicus*' being a junior synonym of *N. persculptus* it is clear that there is considerable diachroneity in the first occurrence of this species. In China and Arctic Canada *N. persculptus* appears as early as just above the *pacificus* Biozone, whilst in Siberia, Kazakhstan and Britain it appears above the *extraordinarius* Biozone.

The *bohemicus* Biozone should be omitted from future graptolite biozonal schemes. Where the first *N. persculptus* appears above the graptolite fauna of the *extraordinarius* Biozone (e.g. Great Britain, Kazakhstan, Siberia) the *persculptus* Biozone consists of the interval between the *extraordinarius* and *acuminatus* biozones (Text-fig. 6).

System	Series	Stage	Scotland Dob's Linn Williams (1983, 1988)	Bohemia Barrandian this paper	Kazakhstan Koren' <i>et al.</i> (1980)	NE Russia Omulev Mountains Koren' <i>et al.</i> (1983)	Canadian Arctic Islands Melchin <i>et al.</i> (1991)	Central China Mu (1988)
SIL	Lland.	Rhudd.						
ORDOVICIAN	Ashgill	Hirnantian	<i>acuminatus</i>	- <i>acuminatus</i> <i>ascensus</i>	<i>acuminatus</i>	<i>acuminatus</i>	<i>acuminatus</i> <i>sinitzini</i> <i>modernii-lubricus</i>	<i>acuminatus</i>
			<i>persculptus</i>	<i>persculptus</i>	<i>persculptus</i> form B	<i>persculptus</i>	<i>persculptus</i>	<i>persculptus</i>
			? <i>extraordinarius</i>	?	? form A	<i>extraordinarius</i>	? 'bohemicus'	'bohemicus'
			<i>anceps</i> <i>pacificus</i>	<i>laticeps</i>	<i>supernus</i>	<i>supernus</i> <i>pacificus</i>	<i>pacificus</i>	<i>uniformis</i> <i>minus</i> <i>typicus</i>
			<i>complexus</i>			<i>longispinus</i>	<i>fastigatus</i>	<i>szechuanensis</i>

TEXT-FIG. 6. Correlation chart summarizing upper Ashgill graptolite biozonations and illustrating the stratigraphical ranges of *Normalograptus persculptus* (solid lines) and *N. extraordinarius* (dashed lines).

In peri-Gondwanan Europe (Bohemia, Saxony, Austrian Carnic Alps, Sardinia) a considerable gap in the graptolite record occurs below the *N. persculptus*-bearing horizon near the top of the Hirnantian. Here, the *extraordinarius* and *pacificus* biozones are entirely (or in Bohemia, almost entirely) represented by strata which are barren of graptolites.

The situation is more complicated in China and the Canadian Arctic where the *bohemicus* Biozone is succeeded by the *persculptus* Biozone. For example, the Chinese *bohemicus* Biozone, containing *N. persculptus* together with a fauna characteristic of the *extraordinarius* Biozone of Britain and the former USSR, could be either (1) assigned to the *extraordinarius* Biozone, despite the presence of *N. persculptus* (applying the assemblage zone concept as used by Elles 1925 and Rickards 1976), or (2) assigned to an expanded *persculptus* Biozone (on the basis that graptolite biozones should be defined by the first appearance of their index species, as suggested by Jaeger 1981, Štorch 1994 and Koren' *et al.* 1995) directly succeeding the *pacificus* Biozone; the *extraordinarius* Biozone would be relegated to subzonal status and would represent the lower portion of the *persculptus* Biozone. We prefer the latter option.

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MORPHOLOGY AND PHYLOGENETIC INFORMATIVENESS OF EARLY ARCHOSAUR BRAINCASES

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ABSTRACT. The braincases of the Triassic early archosaurs *Vjushkovia triplicostata*, *Fugusuchus hejiapensis*, *Xilousuchus sapingensis*, and *Shansisuchus shansisuchus* are described in detail for the first time. A preliminary analysis investigating the phylogenetic informativeness of braincase morphology in the earliest archosaurs incorporates 11 archosauromorph taxa and 17 informative characters. A further seven uninformative and eight problematical braincase characters are discussed. Parsimony and character compatibility permutation tests suggest at the highest possible confidence levels that the data set contains significant hierarchical structure, interpreted as the result of phylogeny. The most parsimonious tree based only on braincase data agrees broadly with existing ideas of early archosaur relationships. However, it conflicts with recently published hypotheses in a number of details, most notably in the presence of a holophyletic Proterosuchia and a well-supported clade of *Erythrosuchus* + *Shansisuchus*. The use of *Prolacerta* as an outgroup does not perturb the parsimonious interpretation of relationship of the included early archosaurs. Topological constraints and additional analyses performed on subsets of the 11 taxa show that some of the hypothesized relationships based only on braincase data are not robust. Unremarkable consistency indices and weakly supported relationships suggest that braincase morphology does not represent an especially informative source of data for the reconstruction of earliest archosaur phylogeny, although this remains an area for further investigation.

ARCHOSAURIA is a major group of diapsids that includes the crocodiles, birds, dinosaurs, pterosaurs, and less well-known forms that together dominated the aerial and terrestrial large vertebrate niches for virtually the whole of the Mesozoic. Understandably, the phylogeny of such a major radiation has attracted considerable attention. All of the many recent studies of the phylogeny of the basal archosaurs (e.g. Gauthier 1986; Benton and Clark 1988; Sereno and Arcucci 1990; Sereno 1991; Parrish 1992, 1993) have excluded some of the more poorly understood earliest forms, and treated the remainder only briefly. Lack of descriptive information for early archosaurs is exemplified by our current knowledge of braincase morphology in these taxa. Indeed, braincase morphology often remains poorly known even in the more derived and generally better understood archosaurs. By virtue of its intricate structure, large number of components, and perceived partial separation from the more obviously functionally adapted parts of the skull, the braincase has been considered to represent perhaps an especially important source of phylogenetic information (e.g. Gow 1975; Parrish 1993). This may be especially true for the early archosaurs, a great number of which have tall, laterally compressed, and superficially similar carnivorous skulls (Gauthier 1986; Parrish 1993).

The aim of this paper is to provide detailed osteological descriptions of the braincases of four poorly known early archosaurs: *Vjushkovia triplicostata*, *Fugusuchus hejiapensis*, *Xilousuchus sapingensis* and *Shansisuchus shansisuchus*. These forms are representatives of the Proterosuchia, a group that includes the very earliest archosaurs and which, upon current understanding (e.g. Benton and Clark 1988; Parrish 1992, 1993), is a paraphyletic grouping of the Proterosuchidae and Erythrosuchidae. The braincase descriptions presented here are based on the thorough observation of original specimens. They are followed by a preliminary attempt to investigate the informativeness of the phylogenetic data that braincase morphology yields. The braincase of *Erythrosuchus* will be

described in detail elsewhere, as will be the endocranial casts of *Erythrosuchus*, *Vjushkovia triplicostata* and *Xilousuchus* (Gower and Sennikov in press).

The taxon Archosauria is applied throughout in its traditional concept, rather than in the crown-group concept advocated by Gauthier (1986). The taxa in the less inclusive Archosauria of Gauthier (1986) are here referred to as 'crown-group archosaurs'.

The abbreviations used for institutional collections are as follows: BMNH, The Natural History Museum, London; BPI, Bernard Price Institute for Palaeontological Research, Johannesburg; GMB, Geological Institute, Beijing; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; PIN, Paleontological Institute of the Russian Academy of Science, Moscow; UMCZ, University Museum of Zoology, Cambridge.

DESCRIPTIVE ACCOUNTS

Vjushkovia triplicostata von Huene (Text-figs 1–3)

Vjushkovia triplicostata is an erythrosuchid from the Yarenga Gorizont (upper part of the Lower Triassic) from the southern Urals of European Russia. It was originally described by von Huene (1960), who studied a syntypic series of specimens from a single site (now a lectotype and many paralectotypes; see Charig and Sues 1976). Von Huene's brief description included only a superficial treatment of the braincase, and comparison with known early archosaurs was minimal. Since the original description, Parrish (1992) has figured part of the braincase of PIN 951-60 and scored *V. triplicostata* for three braincase characters, and Clark *et al.* (1993) have briefly documented the presence and general form of the ossified laterosphenoid. Parrish (1993, fig. 2) has also sketched the route of the internal carotid artery.

The following braincase description and all of the figures are based on the most complete and best preserved specimen, paralectotype PIN 951-60. Information was also obtained from the lectotype PIN 951-59.

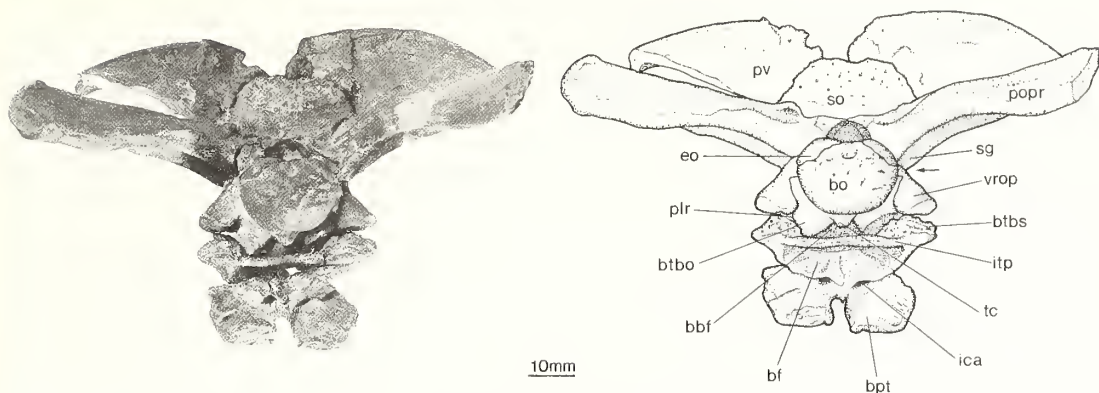
Basioccipital. The basioccipital forms most of the occipital condyle and its dorsolateral corners are excavated to receive the exoccipitals. Posteriorly, it is exposed for a small area on the floor of the foramen magnum, but further forward any exposure on the floor of the main part of the braincase is prevented by midline contact between the overlying exoccipitals. The notochordal pit (Text-fig. 2A) and condylar 'neck' (Text-fig. 2B) are clearly visible.

The basal tubera of the basioccipital are relatively small, simple, and ventrally projecting, and are separated by a smaller, medially positioned tubercle (Text-fig. 1). This is contrary to the information presented by Parrish (1992), who mistakenly identified the ventral rami of the opisthotics as lateral components of the basal tubera of the basioccipital, and listed this as an erythrosuchid synapomorphy (Parrish's character 9). We have observed a clear line of contact between the posterior surface of these two elements.

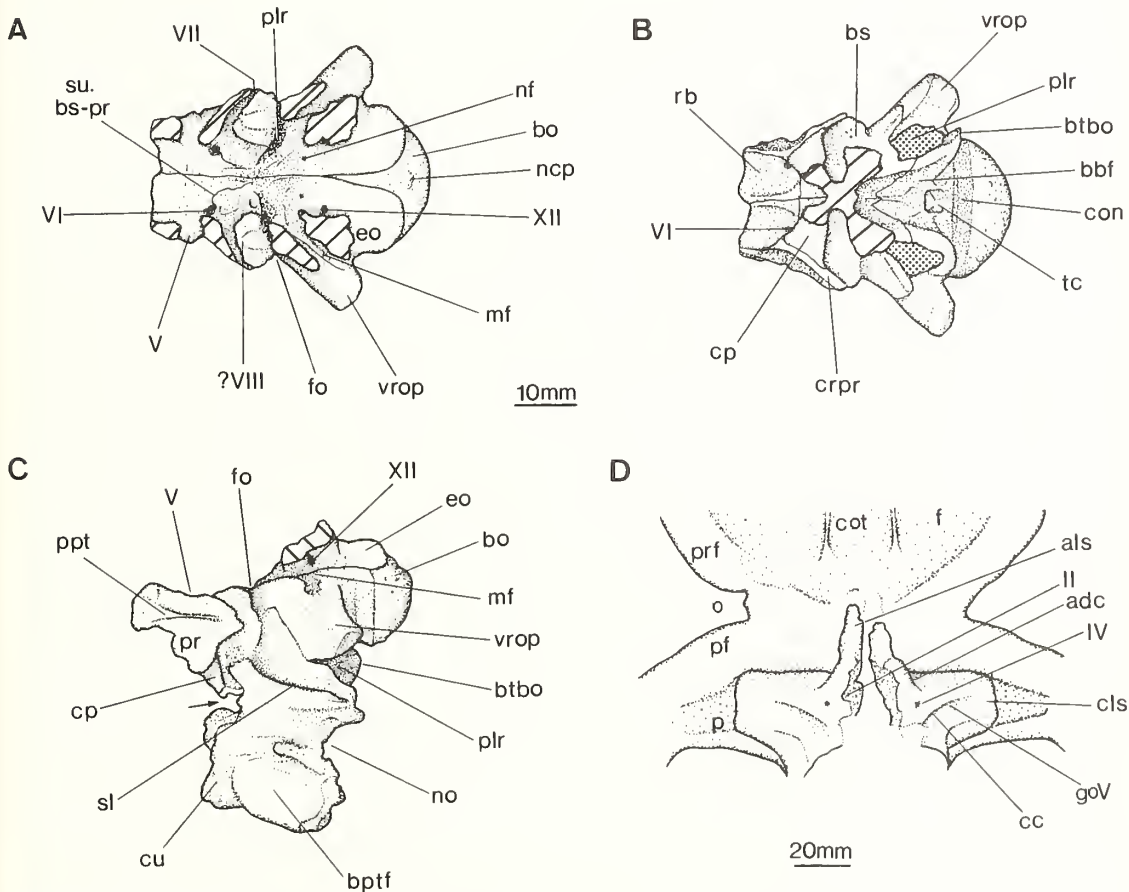
Exoccipital. The exoccipitals meet anteriorly along the midline to exclude the basioccipital from the floor of the endocranial cavity. Posteriorly their medial margins diverge, allowing the basioccipital to form part of the ventral border of the foramen magnum (Text-fig. 2A). At the base of each exoccipital 'pillar' is a single opening for the hypoglossal nerve (XII). Here the exoccipital forms the posterior border of the metotic foramen. The posterodorsal suture with the opisthotic cannot be discerned, although it is probably the exoccipitals which form the majority of the dorsal part of the border to the foramen magnum.

Supraoccipital. The supraoccipital is a shield-like element, excluded from the border of the foramen magnum by dorsomedial contact between the exoccipitals. The posterodorsal surface of the supraoccipital is markedly rugose and the sutures with the parietal, postparietal, and paroccipital process are all simple.

Opisthotic. The opisthotic forms most of the paroccipital process, which has an expanded, angular end with a distal notch. Articulation with the parietal is similar to that in *Erythrosuchus*, with a ventral parietal socket articulating with a dorsal paroccipital projection. The dorsal margin of the paroccipital process lies close to the ventral margin of the parietal, suggesting that the posttemporal fenestra was significantly reduced. The medial end of the posterior surface of the paroccipital process bears a well-defined depression. Within the well-developed stapedia groove the lamellar part of the ventral ramus of the opisthotic separates the metotic



TEXT-FIG 1. *Vjushkovia triplicostata*. Photograph and drawing of posterior and slightly ventral view of braincase of PIN 951/60. Arrow marks main line of fracture dividing specimen into dorsal and ventral portions.



TEXT-FIG 2. *Vjushkovia triplicostata*. A–C. Braincase of PIN 951/60. A, dorsal view of ventral portion, i.e. region below arrow in Text-figure 1. B, ventral view along line of fracture indicated by arrow in C. C, left lateral view. D, ventral view of laterosphenoids and posterior of the skull roof of PIN 951/59.

foramen from the fenestra ovalis. The ventral ramus extends ventrally to form a rounded and dramatically expanded distal end. This stands proud of the crista prootica and is clearly visible in lateral (Text-fig. 2B) and occipital (Text-fig. 1) views. Situated between the distal end of the opisthotic ramus and the dorsal surface of the lateral part of the basisphenoid is an anterodorsally extending channel of unknown function (see below).

Prootic. The posterior part of the prootic forms the anterior face of the proximal end of the paroccipital process. Further anteriorly, the prootic forms a large part of the lateral wall of the braincase and holds the foramen for the exit of the trigeminal nerve (V). Exclusion of the laterosphenoid from the border of the trigeminal foramen is probable, but not certain. A thin but well-defined horizontal ridge is located beneath the simple border of the trigeminal foramen. The crista prootica is not simply curved, but is instead sinusoidal (Text-fig. 2C). The posterior part of this edge, at a point posterior the end of the horizontal ledge described above, holds the apparently single exit foramen for the facial nerve (VII).

The inferior anterior process of the prootic extends forwards for some distance beyond its articulation with the clinoid process of the basisphenoid, before articulating with the laterosphenoid. This freestanding part of the prootic presents a largely ventrally directed surface which holds the exit foramen for the abducens nerve (VI). This foramen lies within a fossa that probably represented the attachment site of the retractor bulbi eye muscles.

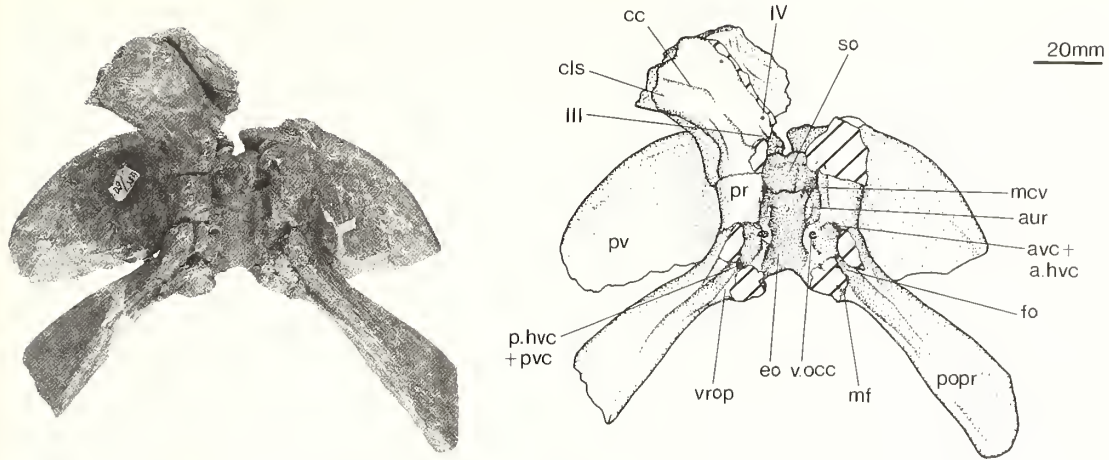
Basisphenoid. The basisphenoid of *V. triplicostata* is similar to that of *Erythrosuchus* in being tall and longitudinally short, and in exhibiting a vertical rather than horizontal alignment of the basal tubera and basiptyergoid processes. Additionally, the lateral surface of the basiptyergoid process and basal tuber are similar in area (Text-fig. 2B). There is little lateral sheathing of the basioccipital by the posterodorsal part of the basisphenoid, because of the presence of the large clubbed end of the ventral ramus of the opisthotic. The posterior edge of the clinoid process harbours a deeply incised groove, which would have transmitted the palatine branch of the facial nerve to a notch between the basisphenoid tuber and the basiptyergoid process, which it would have passed through together with the internal carotid artery. The basiptyergoid process bears an anterolaterally directed, oval facet with a prominent ridge above its posterodorsal end.

The lateral face of the basal tuber is more irregular in form. Anterodorsally it is overlapped by the crista prootica, while posterodorsally it forms a clearly defined contact with the ventral ramus of the opisthotic. The main part of the lateral face of the tuber is dominated by an anteroventrally bordered, curved, and gutter-like groove. This extends from beneath the crista prootica to the posterior edge of the tuber (the dorsal part of this channel is incomplete in PIN 951-60; Text-fig. 2C), and is interpreted as a strongly developed homologue of the 'channel' seen in a similar position on the basisphenoid of *Prolacerta* (termed 'semilunar depression' by Evans 1986).

The posterior surface of the basisphenoid (Text-fig. 1) is complex. The upper surface of the basal tubera are highly rugose and they make simple contact briefly with the ventral rami of the opisthotics and the basal tubera of the basioccipital. A strong horizontal plate extends between the tubera of the basisphenoid, a feature considered to be an erythrosuchid synapomorphy by Parrish (1992, character 10), and referred to here as the 'basisphenoid intertuberal plate'. This plate is emphasized in that it forms the dorsal border to a deep, funnel-shaped fossa, referred to here as the 'basisphenoid fossa'. The dorsal margin of the plate forms a crevice-like concavity with the ventral edges of the basal tubera of the basioccipital. This is referred to here as the 'basioccipital-basisphenoid fossa'. The ventrolateral margins of the basisphenoid fossa are delineated by a second ridge, or more accurately a pair of ridges that do not quite meet along the midline. The ventral edges of these paired ridges harbour the foramina which transmitted the cerebral branches of the internal carotid arteries, from the notches between the basal tubera and basiptyergoid processes to the pituitary fossa. The palatine branches of the internal carotid arteries and facial nerves would have branched off outside these foramina to pass anteriorly to a ventral notch between the two basiptyergoid process. From here they would have continued forward, with the left and right pairs of the nerve and vessel being separated by a low ventral keel. In Parrish's (1993) figure 2A, the feature labelled 'Bp' is not the basiptyergoid process, but rather the basal tuber of the basisphenoid.

The parasphenoid is indistinct suturally from the basisphenoid. The rostrum/cultriform process is incomplete in both PIN 951-59 and 951-60. Its base can be seen between the anterior ends of the basiptyergoid processes of the basisphenoid (Text-fig. 2C). The base is tall and laterally compressed, with a ventral edge that is virtually level with the ventral edge of the basiptyergoid processes.

Laterosphenoid. Clark *et al.* (1993) were the first to record the presence of a laterosphenoid ossification in *V. triplicostata*. This element is also apparent from Tatarinov's (1961) figure 3, despite being identified as an

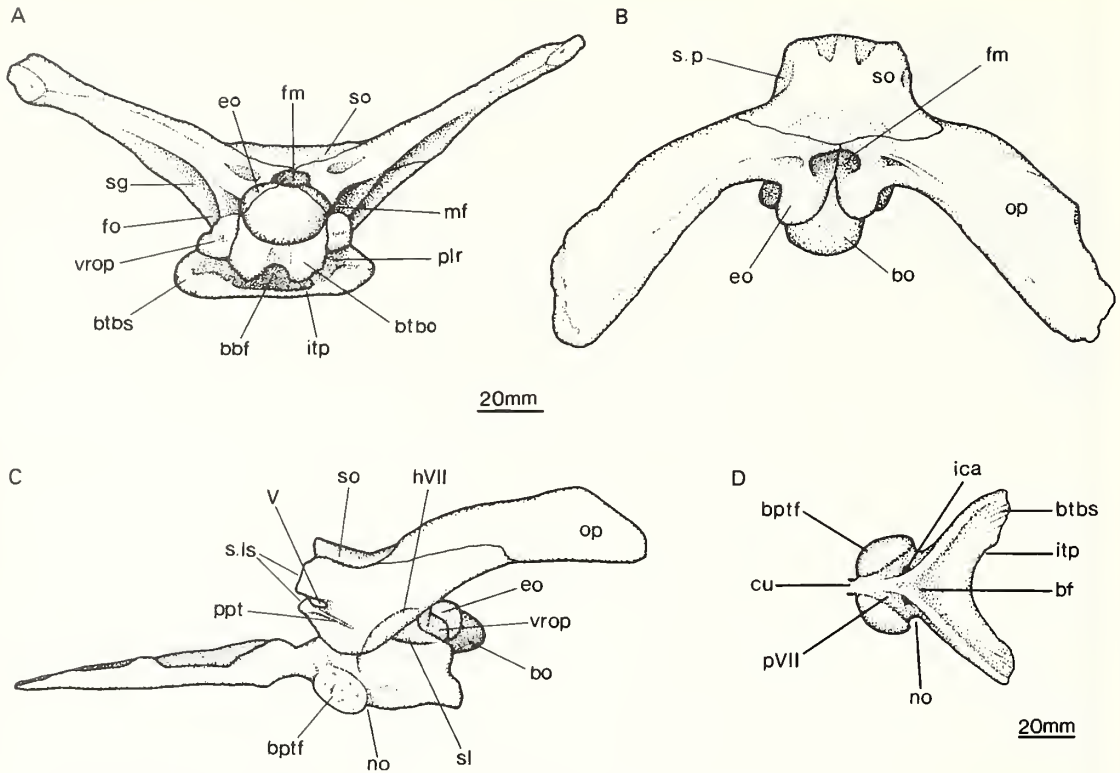


TEXT-FIG 3. *Vjushkovia triplicostata*. Photograph and drawing of ventral view of dorsal portion of braincase of PIN 951/60.

anterior extension of the prootic. Contrary to the statement by Clark *et al.*, the examples in which laterosphenoids are preserved are PIN 951/59 (lectotype, see Charig and Sues 1976; Parrish 1992) and 951/60 (paralectotype). Both of these specimens are dorsoventrally crushed. 951/60 (Text-fig. 3) has lost the anterior processes, and both specimens are ventromedially incomplete. The capitate process bears a strong lateral ridge and a more anterior cotylar crest (Clark *et al.* 1993). A groove lying immediately posterior to this crest would probably have carried the ophthalmic branch of the trigeminal nerve in an anterodorsal direction away from the trigeminal foramen. There is no sign of an epipterygoid pit dorsally, but poor preservation of this area, especially in 951/60, means that this requires verification. The erosion of most of the ventromedial edge in both specimens has made the identification of the position of the exit of the optic (II) and oculomotor (III) nerves difficult. They probably passed through notches seen on the ventromedial edges of the laterosphenoids of 951/59 (Text-fig. 2D), in a position similar to those in *Proterosuchus* and *Erythrosuchus*. A small foramen for the exit of the trochlear nerve (IV) is seen in a position above and lateral to this. The anterior process of the laterosphenoid is longer and more slender than those of *Erythrosuchus*, but without approaching the dimensions seen in *Proterosuchus* (Clark *et al.* 1993). The concavity on the skull roof for the capitate process seems to extend onto the postorbital, but as preserved there is no direct evidence of postorbital-laterosphenoid contact. This area of the specimen is partly repaired and sutures are hard to identify. PIN 951/59 shows that an anterodorsal channel between the parietal and the capitate and anterior processes of the laterosphenoid was present.

As a result of the almost horizontal fracture of specimen PIN 951-60, information can also be presented on the internal surface of the braincase.

Ventral surface (Text-fig. 2A). The basioccipital is exposed on the floor of the posterior part of the foramen magnum as a result of the divergence of the medial margins of the exoccipitals. Further anteriorly the exoccipitals meet along the midline. A single internal foramen where the hypoglossal nerve exited can be seen at the base of each exoccipital pillar. Medial to the anterior margin of the pillars, there is a single pair of nutrient foramina on the floor of the braincase. Just in front of this, the exoccipital slopes down towards the main part of the endocranial cavity. The suture between the exoccipital and opisthotic can be seen on the floor of the metotic foramen, between the front of the pillar and the sectioned ventral ramus of the opisthotic (Text-fig. 2A). The fenestra ovalis is less clearly defined, but lies immediately in front of the ventral ramus of the opisthotic, its anteroventral margin formed by the basisphenoid. The basisphenoid forms most of the central part of the braincase floor. Although the entire course of the exoccipital-opisthotic suture is not discernible, it is certain that medial exposure is not achieved by the basisphenoid. This permits a little prootic-exoccipital contact medially. The basisphenoid forms at least the ventral and posteroventral borders to the channel that carried the facial nerve on a posterolateral route out through the braincase wall.



TEXT-FIG 4. *Fugosuchus hejiapensis*. Braincase of GMB V313 without laterosphenoid. A, posterior and slightly ventral, B, dorsal and C, left lateral views. D, ventral view of basisphenoid.

Immediately behind the posterior wall to the facial nerve channel, the basisphenoid slopes back and down to form a slightly cup-shaped anteroventral border to the largely unossified inner ear region. At the posteroventral limit of this part of the basisphenoid, just inside the fenestra ovalis and along the suture with the exoccipital, there is a crevice running parallel to the facial nerve channel. This crevice, although currently not fully prepared, extends ventrally for a short distance, and would appear to be in a position where an ossified lagenar (cochlear) recess might be found. This area of the braincase floor appears similar to that described for *Plateosaurus* by Galton (1985). There is doubt about identifying this as a lagenar recess because of its absence in *Erythrosuchus*, and the fact that this recess in *V. triplicostata* is weakly defined and continues posteriorly to open out on the occipital surface of the braincase, between the ventral ramus of the opisthotic and the basal tubera of the basioccipital and basisphenoid. Equivalent posterior openings are also seen in, for example, *Proterosuchus* (labelled fenestra ovalis by Broili and Schröder 1934, fig. 6) and *Prolacerta* (Gow 1975, fig. 34). Although an ossified recess is known in crown-group archosaurs, it is only known to be elongated in a restricted group of taxa including birds, crocodiles and dinosaurs (see Walker 1990, p. 111, for a fuller discussion), and in these forms it remains a blind hollow. It is possible that the channel in these plesiomorphic taxa considered here represents an area of residual cartilage, particularly as it is present as a gap between a number of elements that is closed in some closely related taxa. It is here termed the 'pseudolagenar recess'.

Most of the rather flat anterior end of the braincase floor is formed by the prootics which meet along the midline. The abducens foramina pass through the braincase floor from between the trigeminal and facial foramina. While the external abducens foramina are entirely within the prootic, their internal counterparts are positioned on the prootic-basisphenoid commissure.

Dorsal surface (Text-fig. 3). The supraoccipital forms only the anterior part of the ceiling to the endocranial cavity. The exoccipitals form most of the ceiling, although a midline suture between them is not visible.

Posterolaterally, the vestibule is present as a well-defined hollow, the upper part of which holds three unprepared foramina. One is positioned near the broken surface and lies at the posterior limit of the vestibule, interpreted as the posterior opening of the horizontal (or external) and posterior vertical semicircular canals. The posterior ampulla would also have been positioned here. The second opening lies at the same height as this, but in the anterolateral corner of the vestibule. This would have led to the ventral opening of the anterior vertical canal and the anterior opening of the horizontal canal, and would also have held the anterior and external ampullae. The third foramen is situated in the dorsal surface of the vestibule and is interpreted as the ventral limit of the osseus common crus. The medial wall of the otic capsule is not ossified and there is no sign of a foramen perilymphaticum. The auricular recess lies on the medial surface of the thickened wall of the prootic in front of the vestibule. Curving around the dorsal and anterior perimeter of this recess is a groove for the middle cerebral vein, which would have passed through the braincase wall via the trigeminal foramen.

Positive identification of foramina for the acoustic nerve has not been possible. This may be the result of the loss of bone along the line of fracture between the dorsal and ventral parts of the braincase of PIN 951-60, as well as incomplete preparation, but also possibly because they were not ossified. However, a small notch seen immediately outside the anterodorsal limit of the 'pseudolagenar recess' may be a candidate for a possible branch of the acoustic nerve.

Fugusuchus hejiapanensis Cheng (Text-fig. 4)

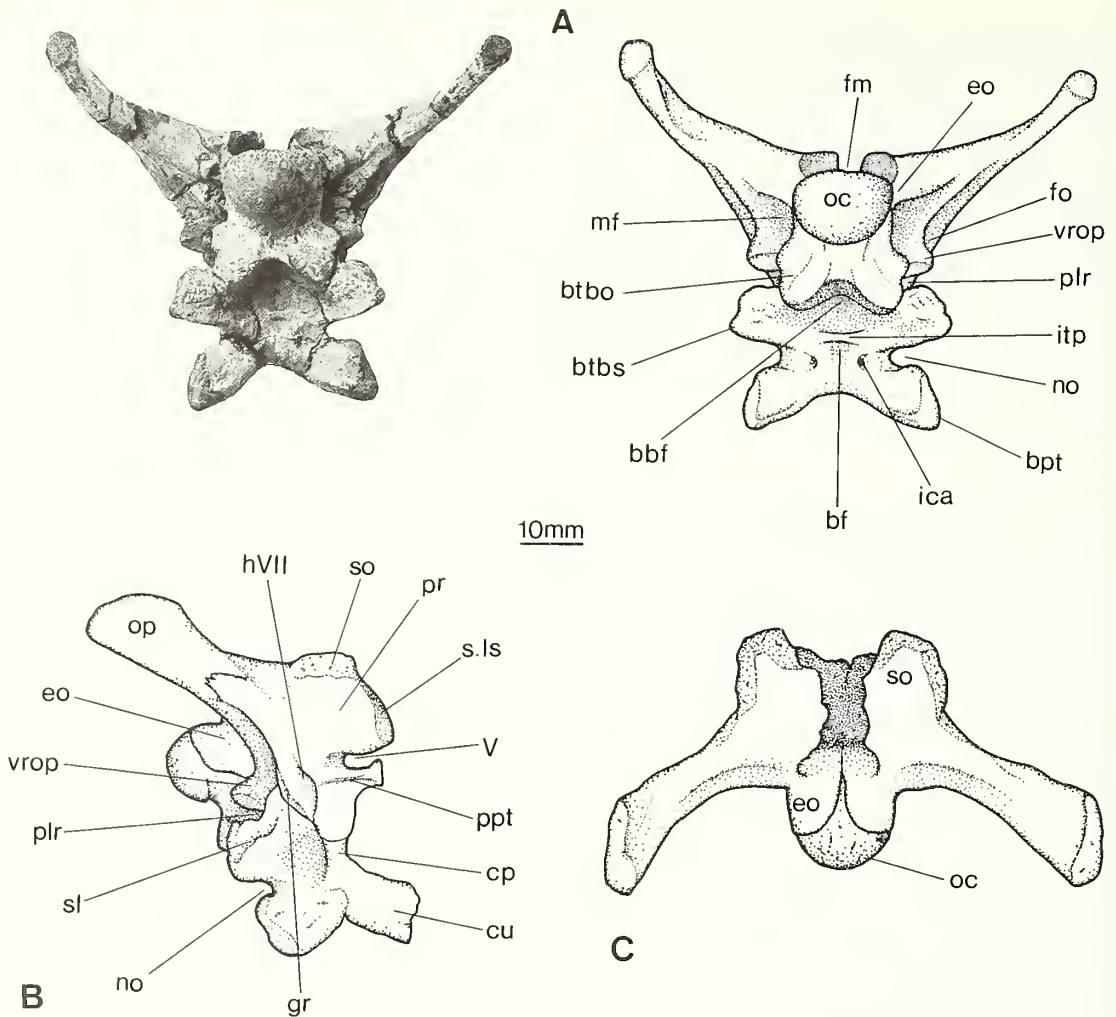
Fugusuchus hejiapanensis is currently known from a single, incomplete specimen (GMB V 313) from the Heshanggou Formation (upper part of the Lower Triassic) of China. It was originally described by Cheng (1980), who identified this taxon as a proterosuchid. He presented only brief notes on the braincase along with a few incompletely labelled diagrams and some unlabelled photographs. Parrish (1992), who postulated that *Fugusuchus* is the most plesiomorphic member of a holophyletic Erythrosuchidae, scored it for three braincase characters but provided no discussion. A redescription of the braincase of *Fugusuchus* is presented here, together with new figures.

The holotype has a well-preserved braincase, free from the rest of the skull and easily studied in three dimensions. The laterosphenoid, preserved but separated from the rest of the braincase (also reported for the early archosaurs *Proterosuchus* and *Euparkeria* by Clark *et al.* 1993), was unfortunately unavailable for examination at the time of this study. There is a slight distortion and relative sliding of some of the elements. Very little detail of descriptive merit could be obtained from the internal surface of the braincase.

Basioccipital. The basioccipital forms most of the condyle, which is fairly elongate when compared with that of other early archosaurs. The basal tubera are a pair of broad, flat, and simple ventral projections that are separated by a shallow, central groove. They do not extend laterally, but instead make contact with the medial edges of the distal ends of the ventral rami of the opisthotics (Text-fig. 4). This is contrary to the description by Parrish (1992), who recorded *Fugusuchus* as having lateral and ventral components to the basal tubera of the basioccipital. As with *V. triplicostata*, he appears to have mistakenly identified the ventral rami of the opisthotics as lateral components of the basal tubera of the basioccipital, when in fact a line of contact is observable between these elements posteriorly. The basioccipital is exposed on the floor of the foramen magnum, but makes no contribution to the ventral surface of the main part of the cerebral cavity.

Exoccipital. The medial margins of the exoccipitals diverge posteriorly on the floor of the foramen magnum, partly exposing the basioccipital (Text-fig. 4B). They meet anteriorly, however, to exclude the basioccipital from the floor of the main part of the braincase. The opposite exoccipitals meet above the foramen magnum, excluding the supraoccipital from the dorsal border of this opening. There is no indication of a suture between the exoccipitals and the opisthotics at the bases of the paroccipital processes. There are well-defined concavities present in this area, just as described above for *V. triplicostata* above. Only one external opening for cranial nerve XII can be seen on the exoccipital, where it forms the posteromedial wall of the metotic foramen.

Supraoccipital. The supraoccipital is a simple shield of bone excluded from the border of the foramen magnum. There are two small V-shaped depressions on the anterior edge of the dorsal surface. The anterolateral part of the supraoccipital, immediately above the point of contact with the prootics, bears facets for articulation with the parietal (Text-fig. 4B).



TEXT-FIG 5. *Xilousuchus sapingensis*. Brainscase of IVPP V6026. A, posterior and slightly ventral, B, right lateral and C, dorsal views.

Opisthotic. The opisthotic forms most of the flat and broad paroccipital process. There is no prominent dorsal process for articulation with the ventral surface of the parietal, although the posttemporal fenestra still seems to have been reduced to what was, at most, a narrow slit. The ventral ramus of the opisthotic is very well developed, stands proud of the crista prootica, and is clearly visible in posterior (Text-fig. 4A) and lateral (Text-fig. 4C) views. The distal end is rounded and greatly expanded.

Prootic. The prootic forms a substantial part of the lateral face of the brainscase. The trigeminal foramen is somewhat crushed, so that the observed suggestion of a laterosphenoid contribution perhaps requires confirmation. The lateral surface of the superior anterior process is featureless, while the inferior anterior process bears a thin horizontal ridge, equivalent to that described for *V. triplicostata*. The margin of the crista prootica follows a regular and simple curve. Near the posteroventral part of the crista prootica, the lateral face of the prootic bears a curved groove which harbours the foramen for the facial nerve. The posterodorsal part of the groove indicates the former path of the hyomandibular branch of the facial nerve, while the anteroventral end was for the palatine branch. The groove for the palatine branch reaches the margin of the

crista prootica, while the hyomandibular branch groove falls just short. The process below the trigeminal foramen has a ventrally facing surface which holds the depression in which the abducens foramen was situated. This area of the braincase is less well preserved, with neither the abducens foramina nor the prootic-basisphenoid suture being detectable.

Basisphenoid. The overall form of the basisphenoid is reminiscent of that of *Proterosuchus* (Cruickshank 1972; Gow 1975), but is unlike that of *V. triplicostata* and *Erythrosuchus*, in that it is horizontally aligned and plate-like. The basiptyergoid processes are in front of, rather than below the basal tubera. Additionally, the lateral surface areas of the basal tubera are greater than those of the basiptyergoid processes (Text-fig. 4c).

Posterodorsally, the lateral faces of the basal tubera bear semilunar depressions, apparently homologous with, but less incised than, those described above for *V. triplicostata*. The clinoid process of the basisphenoid is not particularly well defined. Its posterior margin harbours a groove that would probably have carried the palatine branch of the facial nerve to the notch between the basal tuber and basiptyergoid process.

In ventral view (Text-fig. 4D), the plate-like form of the basisphenoid and its similarity to that of *Proterosuchus* and *Prolacerta* can clearly be seen. Posteriorly, the basal tubera diverge strongly. Between the posterior edge of the basal tubera is a curved plate of bone, homologous to the basisphenoid intertuberal plate described above for *V. triplicostata*. Anteriorly, the approximately hemispherical basiptyergoid processes and facets can be seen, with the base of the cultriform process extending from between them anteriorly. The paired foramina for the cerebral branches of the internal carotid arteries are positioned ventrally and between the posterior ends of the basiptyergoid processes. These foramina are separated along the midline by a ridge that extends forwards and separated the left and right sides of the palatine branches of the facial nerve and internal carotid arteries, right up to the base of the cultriform process of the parasphenoid. The posterior end of this ridge bifurcates, with both branches extending backwards along the anterolateral ventral edges of the basal tubera. This Y-shaped ridge is equivalent to the paired ridges over the carotid foramina of *V. triplicostata*. In *Fugusuchus* the posterior edges of the two branches of this divided ridge form the anterior limit to a concavity on the ventral surface of the basisphenoid, homologous to the funnel-shaped basisphenoid fossa described above for *V. triplicostata*. Despite being a horizontally, rather than more vertically aligned basisphenoid, the arrangement of the ridges and fossae in *Fugusuchus* is essentially the same as that seen in *V. triplicostata*.

In posterior view, the intertuberal plate can be clearly seen. It forms the basioccipital-basisphenoid fossa in conjunction with the basal tubera of the basioccipital. The external opening of the 'pseudolagenar recess' is seen as a narrow hollow between the dorsal surface of the basisphenoid, the ventral edge of the basal tuber of the basioccipital, and the ventral ramus of the opisthotic.

The cultriform process of the parasphenoid is essentially complete. It can be seen in lateral view (Text-fig. 4C) that it tapers smoothly along its length, except for a constriction near its base. The process is U-shaped in transverse section, and has a pointed distal end. The base bears weakly developed lateral grooves that probably indicate the former path of the palatine branches of the facial nerve and internal carotid artery. The parasphenoid is indistinct sutureally from the basisphenoid.

Xilousuchus sapingensis Wu (Text-fig. 5)

Xilousuchus sapingensis, known from fragmentary skull and postcranial material from the Heshanggou Formation (upper part of the Lower Triassic) of China, was originally described by Wu (1981) as a proterosuchid. This taxon has been ignored in all of the recent cladistic analyses of basal archosaur phylogeny. The known braincase material is part of a unique specimen, the holotype IVPP 6026. It is disarticulated from the rest of the very incompletely preserved skull. External preservation is good, but fine detail has not been preserved and/or prepared internally, and the laterosphenoid is absent/missing. Wu (1981) described and figured the braincase briefly and compared it with that of *Proterosuchus*. Corrections, further details and comparisons, and new figures are presented here.

Basioccipital. The basioccipital is a short element closely resembling that of *V. triplicostata*, *Fugusuchus* and *Proterosuchus* (Cruickshank 1970) in that the exoccipitals prevent it from contributing to the anterior part of the braincase floor, but is exposed further posteriorly on the floor of the foramen magnum. The basal tubera are large, bilobed, strongly diverging, and separated by a broad notch (Text-fig. 5A). The ventral surface of the basal tubera of the basioccipital contribute to the basioccipital-basisphenoid fossa, which is larger than in the other taxa described here.

Exoccipital. Anteroventrally, the medial margins of the exoccipitals meet along the midline, but posteriorly they diverge (Text-fig. 5c). The dorsal part of the exoccipital is indistinct suturally from the opisthotic. The dorsal border of the foramen magnum is incomplete, leading to uncertainty over whether or not the exoccipitals meet along the midline to exclude the supraoccipital from its border. A relatively large area of the lateral surface of the exoccipital is exposed, and there is a single opening for the hypoglossal nerve.

Supraoccipital. The supraoccipital is firmly attached to the rest of the braincase and its suture with the base of the paraoccipital process cannot be detected. The central part of the supraoccipital is missing, so that the possibility of contribution to the dorsal border of the foramen magnum, or to an occipital peg, is currently unknown.

Opisthotic. The opisthotic forms most of the paroccipital process, which has an expanded, rounded, and unnotched distal end. There is no indication of a process on the dorsal edge of the paroccipital process which might have articulated with the ventral surface of the parietal (as seen in *Erythrosuchus* and *V. triplicostata*). Posteromedially, the bases of the paroccipital processes are shallowly concave, but the depressions are not as well defined as in *V. triplicostata* or *Fugusuchus*.

Between the metotic foramen (which probably would have transmitted cranial nerves IX, X, XI, and not X, XI, XII as suggested by Wu 1981) and the fenestra ovalis, the ventral ramus of the opisthotic projects downwards and ends distally in a much expanded, club-like tip. This stands proud of the crista prootica and is clearly visible in posterior and lateral views. The distal end of the ventral ramus of the opisthotic is surrounded by three openings: the fenestra ovalis and metotic foramen above, and the posterior opening of the 'pseudolagenar recess' below. Posteriorly, the ventral ramus of the opisthotic articulates with the basal tubera of the basioccipital, while anteriorly its base is sheathed laterally by the basisphenoid.

Prootic. The posterior part of the prootic forms the anterolateral surface of the base of the paroccipital process, its suture with the opisthotic being not entirely clear. The rest of the prootic forms much of the lateral face of the braincase (Text-fig. 5b). The dorsal area of the lateral face of the prootic bears an anteroventral-posterodorsal groove, which widens and deepens posteriorly. This may be associated with the posttemporal fenestra.

The trigeminal foramen would have been formed by the laterosphenoid (if present) as well as the prootic. The lateral surface of the superior anterior prootic process is smooth and featureless. The inferior anterior process is much smaller, has an upturned anterior end, and bears a thin horizontal ridge on its lateral surface. Immediately behind the trigeminal foramen is a well-defined and posteriorly directed concavity of unknown function. The anterior surface of both of the anterior prootic processes are roughened and would have articulated with the laterosphenoid (if present). The ventral surface of the inferior process holds downward-facing concavities, in which the prootic forms the entire border of the abducens exit foramen. This is contrary to Wu's (1981) description of the position of the abducens foramina as within the basisphenoid.

The foramen for the facial nerve lies within a curved groove behind and below the trigeminal opening. The posterodorsal end of the groove (for the hyomandibular branch of the facial nerve) dies out on the lateral prootic surface, while the ventral part (palatine branch) continues to the posteroventral edge of the crista prootica. The crista prootica is like that of *V. triplicostata* in being sinusoidally curved. Part of its edge carries a fine groove, extending between the stapedial groove and the groove for the palatine branch of the facial nerve.

Basisphenoid. The basisphenoid of *Xilousuchus* forms a large part of the braincase. It is essentially a vertically aligned element and, viewed laterally (Text-fig. 5b), the basal tubera and basiptyergoid processes are of similar size. The dorsal limit of the basal tuber extends up between the crista prootica and the distal end of the ventral ramus of the opisthotic. Its lateral face bears the semilunar depression, which is not particularly strongly incised, and is perhaps unusual in being sinusoidal, running parallel to the dorsal border of the basal tuber.

Between the basal tuber and the basiptyergoid process there is a well-developed notch for the passage of the internal carotid artery and palatine branch of the facial nerve. The basiptyergoid facet is sub-triangular. Anterodorsally, the basisphenoid forms a well-defined clinoid process that articulates with the anteroventral edge of the prootic. Its posterior edge forms the anterior margin of a deep depression that meets the two grooves on the edge of the crista prootica, described above. This depression curves back and becomes shallower, and its anterior margin probably would have harboured the palatine branch of the facial nerve on its way to the notch between the basal tuber and basiptyergoid process. Although relatively large and deeply

incised, this depression does not hold a foramen for the passage of the cerebral branch of the internal carotid artery as described by Wu (1981); rather this foramen is on the posteroventral surface of the basisphenoid. Deep depressions on the lateral surface of the basisphenoid of some more derived archosaurs may be associated with pneumatic recesses of the tympanic cavity (see e.g. Chatterjee 1991).

In posterior view, the ventral ramus of the opisthotic is seen not to make substantial contact with the dorsal surface of the basal tubera of the basisphenoid, and the resultant gap forms the external opening of the 'pseudolagenar recess'. The basisphenoid intertuberal plate is only weakly developed. The basisphenoid fossa below it is considerably smaller and shallower than the basioccipital-basisphenoid fossa above it. Low, paired ridges that extend a short distance medially from the posteroventral edges of the basal tubera in the direction of the internal carotid foramina, represent the equivalent of the medially incomplete second ridge in *V. triplicostata* and the Y-shaped ridge in *Fugusuchus*. The foramina carrying the cerebral branches of the internal carotid arteries to the pituitary fossa are positioned posteriorly, close to the notches between the basiptyergoid processes and basal tubera of the basisphenoid. The path of the palatine branches of the internal carotid artery and facial nerve is not well defined. There is, apparently, no ventral keel separating the left and right pairs of these elements. The posterior and ventral edges of the basiptyergoid processes are noticeably thickened.

The parasphenoid is suturally indistinct from the basisphenoid. The cultriform process of the holotype is incomplete. The proximal end is not particularly deep, so that it is not confluent with much of the anterior edge of the clinoid process of the basisphenoid. There is no indication of the proximal constriction that is seen in *Fugusuchus*. The transverse section is V-shaped. Posteriorly, at the base, the dorsal surface shows a well-defined pituitary fossa housing the anterior foramina for the internal carotid arteries.

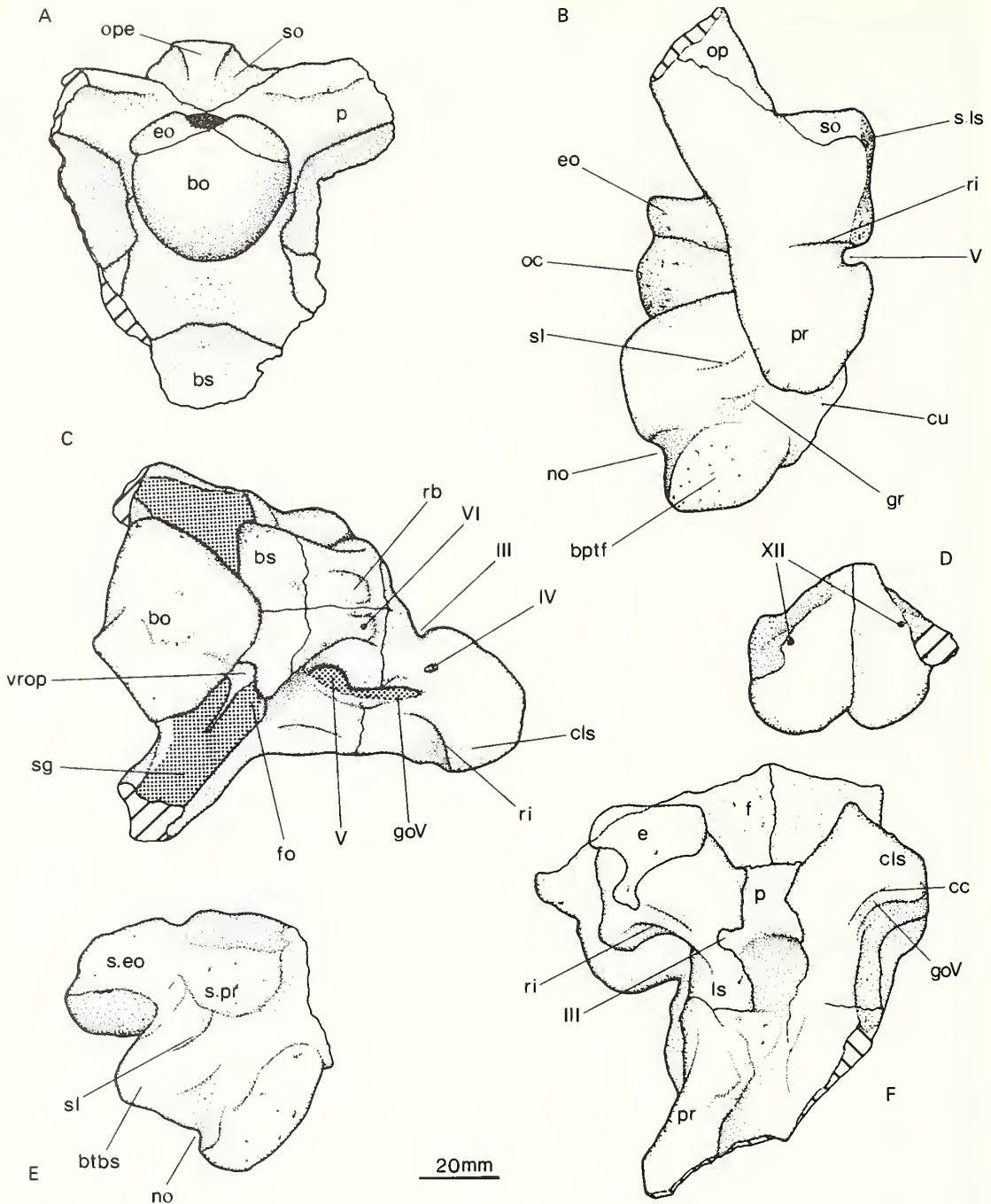
Shansisuchus shansisuchus Young (Text-fig 6)

Shansisuchus shansisuchus is an erythrosuchid originally described by Young (1964), from a large amount of material collected from Upper Ehmaying (Middle Triassic) deposits in China. Young briefly described the braincase only of the paratype IVPP V2501 and figured this and another, unnumbered specimen (field collection 56173). Since this work, the braincase of *S. shansisuchus* has received little further attention. Cruickshank (1970) understood from Young's information that a laterosphenoid was absent. Parrish (1992) scored *S. shansisuchus* for three braincase characters without detailed discussion. Clark *et al.* (1993) noted the apparent presence of a laterosphenoid in Young's (1964) figure 6.

Apart from the two specimens figured by Young (1964), there are, among the paratype material (mostly under field collection no. 56173), at least some further 17 fragmentary specimens, all of which are incompletely prepared. The most complete braincase, belonging to IVPP V2501, has now unfortunately been obscured by plaster, paint, and metal during the course of mounting for display. However, information has been pieced together from the other fragmentary specimens, and a detailed description of the external surface of most of the braincase is now possible. No braincase material has been referred to the other two named species of *Shansisuchus*. In terms of their known morphology, *S. heiyoukouensis* (Young 1964) and *S. kuyeheensis* (Cheng 1980) appear to be indistinct from *S. shansisuchus*.

Basioccipital. The basioccipital is very similar to that of *Erythrosuchus*. It is completely excluded from the floor of the cerebral cavity and foramen magnum. The occipital condyle is directed posteroventrally and the condylar neck is weakly defined. The basal tubera are broad, simple, and diverge quite strongly. They overlap the dorsal part of the basal tubera of the basisphenoid and their posterior surface is shallowly concave. They are not composed of medial and lateral parts as recorded by Parrish (1992, table 2).

Exoccipitals. The exoccipitals are the same as in *Erythrosuchus* in that they meet along the midline on the floor of the cerebral cavity, and their medial margins do not diverge posteriorly on the floor of the foramen magnum. They also meet dorsally (Text-fig. 6A) to exclude the supraoccipital from the border of the foramen magnum. Here the exoccipital bears a simple facet for the proatlas. The exoccipital is indistinct suturally from the opisthotic at the base of the paroccipital process. The posterior surface of the base of the paroccipital process is concave, but this depression is not as marked as that seen in *V. triplicostata*. No specimen currently shows very clearly the area of the exit of the hypoglossal nerve. Two specimens showing the internal area of this exit indicate that there was a single foramen on each side of the braincase (Text-fig. 6D).



TEXT-FIG 6. *Shansisuchus shansisuchus*. Various IVPP braincase specimens; field collection 56173. A, posterior and slightly ventral view of braincase; B, right lateral view of braincase of IVPP V 2511; C, ventral view of crushed braincase; D, dorsal view of isolated exoccipitals; E, right lateral view of isolated basioccipital and basisphenoid; F, ventral view of laterosphenoids and posterior part of skull roof.

Supraoccipital. The supraoccipital is essentially similar to that of *V. triplicostata*, except notably in that it makes a large contribution to the posteriorly projecting occipital peg (Text-fig. 6A), which in *V. triplicostata* is formed solely by the postparietal. The supraoccipital of *Shansisuchus* also forms a small part of the ceiling to the endocranial cavity.

Opisthotic. The opisthotic forms most of the paroccipital process, the distal end of which is incompletely known. The dorsomedial edge of the paroccipital process bears a projection which articulates with a well-defined notch on the ventral edge of the posterolateral process of the parietal. This suggests that the posttemporal fenestra was considerably reduced.

The opisthotic forms the border between the metotic foramen and the fenestra ovalis with a thin lamella of bone, the ventral ramus of the opisthotic. This is similar to that of *Erythrosuchus*, but different to those of *V. triplicostata*, *Fugusuchus* and *Xilousuchus*, in that it is much reduced and does not stand proud of the crista prootica or have a greatly expanded distal end that is visible in lateral and posterior views. Furthermore, there is no indication of an equivalent of the posterior end of the 'pseudolagenar recess' between the ventral ramus and the basal tubera, such as described for the other three taxa above.

Prootic. Posteriorly the prootic forms the anterior surface of the proximal end of the paroccipital process, as shown in Text-figure 6B. The lateral surface of the superior anterior prootic process bears an approximately horizontally aligned brow over the trigeminal foramen. The inferior process resembles that of *Erythrosuchus* more than that of either *V. triplicostata* or *Xilousuchus*, in that the margin of the crista prootica is simple (the specimen in Young's fig. 5 is eroded in this area) and there is no horizontal ridge below the trigeminal foramen. The crista prootica also sheaths laterally the ventral ramus of the opisthotic. Beneath where the inferior process articulates with the laterosphenoid, the prootic bears the depression which houses the exit for the abducens nerve. This area, in *Shansisuchus*, is anteriorly facing (the specimen shown in Text-fig. 6C has been strongly crushed in this area). It is not well preserved and/or prepared in any specimen.

Basisphenoid. The basisphenoid of *Shansisuchus* is a vertically aligned element that is very similar in overall form to that of *Erythrosuchus*. The basal tubera of the basisphenoid are positioned above the oval facets of the comparably sized basiptyergoid processes. All of the expected features are present, but they are not well defined. The clinoid process is a low relief feature, and the semilunar depression is only faintly discernible on the lateral surface of the basal tuber. Correspondingly, the lateral groove for the palatine branch of the facial nerve is only weakly incised. This groove widens and deepens posteriorly, to form a broad notch that transmitted the internal carotid artery and facial nerve to the posteroventral surface of the basisphenoid.

The posterior surface of the basisphenoid is poorly known because of the incomplete preservation and preparation of a number of specimens. The dorsal part is substantially overlapped by the tubera of the basioccipital (Text-fig. 6A), and immediately ventral to this is the least well known area of the basisphenoid. The lack of a well preserved and/or prepared posterior basisphenoid surface means that there is currently no evidence for the presence of an intertuberal plate (*contra* Parrish 1992). The paired foramina for the internal carotid arteries are situated on the posteroventral surface, beneath a ridge of bone and close to the notches between the basal tubera and basiptyergoid facets.

The suturally indistinct parasphenoid of *Shansisuchus* is unknown except for the laterally compressed base of the cultriform process. It is remarkably tall, with the dorsal part being overlapped by the crista prootica and the ventral edge extending below the dorsal margin of the basiptyergoid facet (Text-figs 6B, E).

Laterosphenoid. There has been much uncertainty over the presence of a laterosphenoid ossification in the braincase of *Shansisuchus*, perhaps because of the lack of first-hand information. The paratype material, however, includes several specimens which confirm its expected presence. It still remains poorly known, with the best examples currently being two incomplete and strongly crushed specimens (Text-figs 6C, F).

The laterosphenoid is very similar to that of *V. triplicostata* and *Erythrosuchus*, particularly in being of robust construction. The capitate process is particularly thick and there is a strong ridge running up its lateral edge. The anterior process is incomplete in both specimens, but does not appear to have been either long or slender. Because of compression and erosion it is not possible to assess the possibility of the presence of an 'anterodorsal channel' between the capitate and anterior processes, such as is seen in *V. triplicostata* and *Erythrosuchus*. The anteromedial margin is the least well preserved part of these two specimens, so that the location of an exit foramen for cranial nerve II has not been positively identified. A well-defined notch seen in the medial margin of the laterosphenoid and near the laterosphenoid-prootic suture, was probably for the

passage of cranial nerve III. The only sign of a possible exit foramen for cranial nerve IV is an incompletely prepared pit on the anteroventral surface of the specimen illustrated in Text-figure 6G. A groove immediately posterior to the weakly defined cotylar crest probable carried the ophthalmic branch of the trigeminal nerve. The posterior end of this groove is deeply incised, so that the unprepared trigeminal foramen appears to be long, narrow, and formed by the laterosphenoid as well as the prootic (Text-fig. 6c).

PHYLOGENETIC IMPLICATIONS

The taxa and characters

The descriptions above give an indication of several braincase characters that might be of use in a study of early archosaur phylogeny. A preliminary attempt was made to investigate the phylogenetic informativeness of braincase morphology by constructing a data matrix of phylogenetic characters for representative early archosaur taxa. The selected taxa were those that have adequately known braincase material. Three crown-group archosaurs were selected, based on the criterion of availability of detailed, published braincase descriptions. *Prolacerta* was included as a non-archosaurian representative.

The 11 taxa used (with the sources of the information, where not only from our own observations, given in parentheses) are: *Prolacerta* (Gow 1975; Evans 1986); *Proterosuchus* (Cruickshank 1970, 1972; Gow 1975; Clark *et al.* 1993); *Fugusuchus* (Cheng 1980); *Xilousuchus*; *Vjushkovia triplicostata*; *Erythrosuchus*; *Shansisuchus*; *Euparkeria* (Cruickshank 1970, 1972; Evans 1986; pers. obs. of UMCZ T692); *Sphenosuchus* (Walker 1990); *Parasuchia* (Camp 1930; Chatterjee 1978); *Stagonolepis* (Walker 1961, 1990, pers. comm.).

Characters were selected on the basis of informativeness with respect to the taxa employed. The definition of states of the 17 characters that were deemed suitable are listed below.

Characters included in analysis. These are included on the criteria of an informative distribution of character states among the taxa included, as well as discrete states being clearly recognizable.

1. Position on basisphenoid of foramina for the cerebral branches of the internal carotid arteries leading to the pituitary fossa (ventral/posteroventral = 0; lateral = 1). The plesiomorphic condition for archosaurs is for the internal carotid foramina to be in a ventral (e.g. *Prolacerta*, *Proterosuchus*) or posteroventral (*V. triplicostata*) position, on the external surface of the braincase. The posteroventral position is also seen in *Euparkeria* (pers. obs. of UMCZ T692). The foramina in more derived archosaurs (e.g. *Stagonolepis* Walker 1961; Parrish 1993; *Postosuchus* Chatterjee 1985; *Parasuchus* Chatterjee 1978; *Massospondylus* Gow 1990) are positioned on the lateral surface of the basisphenoid. Parrish (1993, character 7) appears to have been the first to use this character in reconstructing basal archosaur phylogeny. However, the scoring of this character by Parrish (1993, table 2) for many of his included taxa is contradicted by his discussion in the text (1993, p. 289), and by his comment that a lateral position of the foramina is a synapomorphy of proterochampsids + crown-group archosaurs (*Euparkeria* is incorrectly scored as exhibiting the lateral position; *Chanaresuchus*, *Erythrosuchus*, *Proterosuchus*, and all crown-group archosaurs except *Riojasuchus* are scored as exhibiting the posteroventral position). In the plesiomorphic condition, the proximity of these paired foramina to the midline shows some variation and may also be phylogenetically informative.
2. Basisphenoid intertuberal plate (present = 0; absent = 1). The presence of a plate between the basal tubera of the basisphenoid was interpreted by Parrish (1992) as an erythrosuchid synapomorphy. It has been shown above that this plate is apparently homologous with one present on the horizontally aligned basisphenoids of, for example, *Prolacerta*, *Proterosuchus*, and *Fugusuchus* (correctly scored by Parrish). The state is currently unknown in *Shansisuchus*. In *Erythrosuchus* and *Xilousuchus* the plate is present as a much reduced feature. Equivalent structures have yet to be identified in other archosaur taxa, including *Euparkeria*.
3. Elements enclosing abducens foramen (basisphenoid and prootic = 0; within prootic only = 1). In early archosaurs and immediate outgroups, such as *Euparkeria*, *Proterosuchus* and *Prolacerta*, the external foramina for the abducens nerves lie between the basisphenoid and prootics. This is also the case in some more derived archosaurs such as *Parasuchus* (Chatterjee 1978). In *Erythrosuchus*, *V. triplicostata*, *Xilousuchus*, and *Shansisuchus*, however, the external abducens foramina are held entirely within the prootic. An additional state of 'abducens foramina within basisphenoid only', could be added, but in this analysis would be uninformative as it is seen only in *Sphenosuchus* (Walker 1990). The relationship of this third state to the others is uncertain

and so *Sphenosuchus* is coded as equivocal in this analysis. In *Erythrosuchus*, the internal exit foramen for the abducens nerve is also held entirely by the prootic, while in *V. triplicostata* this lies between basisphenoid and prootic. 'External abducens foramina held by prootic only' may therefore be an erythrosuchid synapomorphy, with *V. triplicostata* retaining the plesiomorphic condition internally.

4. Position of external abducens foramina (on an anterior = 0; or ventral = 1 surface). In *Prolacerta*, *Proterosuchus*, and *V. triplicostata*, the external abducens foramina are positioned on the horizontal ventral surface of the inferior anterior prootic process. In *Erythrosuchus*, *Shansisuchus*, and some non-erythrosuchid archosaurs, such as *Parasuchus* and possibly *Euparkeria*, the external exit foramina for the abducens nerves lie on a vertical, upturned anterior surface of the front of the braincase.

5. Ventral ramus of the opisthotic (prominent = 0; recessed = 1). In immediate archosaur outgroups, as well as *Proterosuchus*, *Euparkeria*, *Fugusuchus*, *Xilousuchus* and *V. triplicostata*, the lamellar part of the ventral ramus of the opisthotic is very prominent, making it clearly visible in lateral and posterior views. In *Erythrosuchus* and *Shansisuchus*, the ventral ramus is poorly developed and does not stand proud of the stapedia groove. The ramus is also reduced in phytosaurs (Camp 1930; Chatterjee 1978), but it is not recessed within a deep stapedia groove, and remains visible in lateral view.

6. Ridge on lateral surface of inferior anterior prootic process below trigeminal foramen (present = 0; absent = 1). The presence of this feature has been described above in *V. triplicostata*, *Fugusuchus* and *Xilousuchus*. It can also be seen in immediate archosaur outgroup taxa, such as *Hyperodapedon* (Benton 1983) and *Prolacerta* (Gow 1975). It is perhaps the dorsalmost part of the area of origin of the protractor pterygoidei, such as in the extant taxon *Ctenosaura* (Oelrich 1956, p. 45, fig. 35).

7. Basisphenoid (horizontally = 0; or more vertically = 1 oriented). *Prolacerta*, *Proterosuchus*, and *Fugusuchus* all have a horizontally aligned basisphenoid. Erythrosuchids, *Euparkeria*, and a range of more derived archosaurs show some degree of verticalization of this element, with the basipterygoid processes positioned ventral as well as anterior to the basal tubera. The condition in phytosaurs is difficult to interpret from published figures. The presumably plesiomorphic condition (horizontal) is apparently retained/reversed in some derived archosaurs (e.g. *Massospondylus* Gow 1990, *Lewisuchus* Romer 1972 and birds Chatterjee 1991).

8. Crista prootica outline (simply curved = 0; sinusoidal = 1). Most early archosaur taxa exhibit a regular and simply curved free edge to the crista prootica as seen in lateral view. *V. triplicostata* and *Xilousuchus*, as described above, show a sinusoidally curved edge.

9. Prootic midline contact on endocranial cavity floor (absent = 0; present = 1). Evans (1986) pointed out that archosaurian outgroup taxa such as *Prolacerta* and rhynchosaurs lack any midline contact between the opposite prootics on the endocranial cavity floor. *Erythrosuchus*, *V. triplicostata*, *Shansisuchus*, and probably *Xilousuchus*, all exhibit such contact.

10. Basisphenoid midline exposure on endocranial cavity floor (present = 0; absent = 1). In the majority of taxa studied, the absence of midline exposure of the basisphenoid on the floor of the endocranial cavity is consistently linked with the presence of prootic midline contact. The condition seen in *Parasuchus* (Chatterjee 1978), however, shows that these two features do not always coincide. The plesiomorphic condition, as seen in e.g. *Hyperodapedon* (Benton 1983), is apparently the presence of midline basisphenoid exposure.

11. Semilunar depression (present = 0; absent = 1). The groove, currently of unknown function, described on the lateral surface of the basal tubera of the basisphenoid of *Prolacerta*, was termed 'semilunar depression' by Evans (1986). An apparently homologous groove has been found in the taxa described above, and is also present in *Erythrosuchus*, *Proterosuchus* (Gow 1975, fig. 25), and *Euparkeria* (pers. obs. of UMCZ T692). The apparent absence of this feature in extant diapsids means that discovering the function of this feature is currently extremely problematical. This does not, however, prevent it from being a potentially informative feature for phylogenetic analysis.

12. Laterosphenoid anterodorsal channel (absent = 0; present = 1). The anterodorsal channel, seen between the anterior and capitale processes of the laterosphenoid and the parietal in *Erythrosuchus* and *V. triplicostata* is currently of unknown function. It is absent in *Proterosuchus* but unknown in the other early archosaurs considered here. Whatever its function, its position and form might currently be interpreted as a synapomorphy of a group including, at least, *Erythrosuchus* and *V. triplicostata*.

13. Parasphenoid cultriform process (simple = 0; dorsoventrally constricted towards the base = 1). In lateral view, the base of the cultriform process of the parasphenoid may be constricted, before expanding slightly and eventually tapering anteriorly. This is seen in *Proterosuchus* (Cruickshank 1972) and *Fugusuchus* (see above), but not in *Prolacerta* (Gow 1975) or *Xilousuchus* (see above). Unfortunately this area is not well preserved in a number of other early archosaurs.

14. 'Pseudolagenar recess' between ventral surface of the ventral ramus of the opisthotic and the basal tubera (present = 0; absent = 1). This channel is of unknown function. Its anterodorsal limit, in *V. triplicostata*, is

seen to be in a position approximately relating to that where an ossified lagenar recess might be found. However, the posterior continuation of this channel between at least three elements, and the fact that it is closed in closely related taxa, suggests that a more plausible interpretation is that it represents an area of residual cartilage. An unossified gap is also seen between braincase elements in, for example, extant and extinct spheodontians (Wu 1994). The 'pseudolagenar recess' is seen in *Prolacerta* (Gow 1975, fig. 34), *Proterosuchus*, *Euparkeria* (pers. obs. of UMCZ T692), *V. triplicostata*, *Fugusuchus*, and *Xilousuchus*. The absence of this channel in *Erythrosuchus* and *Shansisuchus*, or at least its not opening externally, would seem to be paralleled in more derived, crown-group archosaurs.

15. Base of cultriform process of parabasisphenoid (relatively short dorsoventrally = 0; tall, with the dorsal edge extending up between clinoid processes and ventral part of cristae prootica = 1). In *Prolacerta*, the base of the cultriform process is not tall and does not extend up between the anterior edges of the clinoid processes of the basisphenoid. This condition is seen also in *V. triplicostata*, *Fugusuchus* and *Xilousuchus*. In *Shansisuchus* and *Erythrosuchus*, the base of the cultriform process is proportionately much taller, and the dorsal edge extends up between the clinoid processes. The latter condition is also seen in crown-group taxa including *Machaerops* (Camp 1930) and *Stagonolepis* (Walker 1961). We also consider it to be present in *Sphenosuchus*, although the parabasisphenoid as a whole is much derived over that seen in earlier archosaurs.

16. Number of hypoglossal foramina (two = 0; one = 1). While all of the taxa described above have only a single foramen for the hypoglossal nerve, this is not the condition present in all archosauromorph taxa. Two foramina are not uncommon and have been reported in *Euparkeria* (Cruickshank 1970), *Paradapedon* (Chatterjee 1974), *Parasuchus* (Chatterjee 1978), *Hyperodapedon* (Benton 1983), *Prolacerta* (Evans 1986) and *Sphenosuchus* (Walker 1990). Extant crocodilians have been one and three foramina (Iordansky 1973).

17. Medial margin of exoccipitals (do not make contact = 0; make contact for majority of their length = 1; meet anteriorly, but diverge posteriorly = 2). In *Prolacerta* (Gow 1975; Evans 1986), the opposite exoccipitals do not make contact along the midline of the braincase floor, allowing exposure of the basioccipital here. This is also the condition in a number of relatively derived archosaurs (e.g. living crocodilians, Iordansky 1973; *Sphenosuchus*, Walker 1990). In all of the taxa described above, as well as in *Erythrosuchus*, the exoccipitals make substantial contact along the midline to prevent exposure of the basioccipital on the braincase floor. Midline exoccipital contact is also seen in *Parasuchus* (Chatterjee 1978).

In *Prolacerta*, and also in archosaur outgroup taxa where the exoccipitals meet along the midline (e.g. *Hyperodapedon* Benton 1983), the medial margins of the exoccipitals are parallel to one another. In *V. triplicostata*, *Fugusuchus* and *Xilousuchus*, the posterior part of the medial exoccipital margins diverge to expose the dorsal surface of the basioccipital.

Although the divergence of the medial margins of the exoccipitals is possibly logically independent from the presence of midline contact, lack of contact and divergence are not known to occur together. Treating this as two separate binary characters (presence/absence of contact; presence/absence of posterior divergence) would effectively order the acquisition of the derived states (0-1-2) of the character defined here. Further investigation of this character may shed some light on its possible association with other characters. *Hyperodapedon*, for example, exhibits midline exoccipital contact but also anteroventral exposure of the basioccipital (Benton 1983).

Several potential characters were removed from the analysis *a priori*, either because they are uninformative in the context of this preliminary analysis, or because they are problematical in terms of recognizing discrete states.

Uninformative characters. These include characters with an uninformative distribution of states among the taxa included in this analysis (at least one of their states present in fewer than two taxa), as well as characters that are here interpreted as autapomorphic for particular early archosaurs. Only those characters of relevance to the earliest archosaurs are discussed here.

18. Presence of a laterosphenoid. The presence of an ossified laterosphenoid was formerly thought to be a synapomorphy only of the crown-group archosaurs, but Clark *et al.* (1993) have shown it to be present in all archosaurs (their Archosauriformes). Disarticulation of the laterosphenoid from the rest of the braincase is apparently common in early archosaurs (see above and Clark *et al.* 1993), making it difficult to confirm the absence of this element in specimens represented by disarticulated cranial remains. This character is uninformative in the present analysis because only *Prolacerta* is known to lack a laterosphenoid.

19. Laterosphenoid-postorbital contact. This contact is present in the crown-group archosaurs employed in

this analysis, as well as in *Erythrosuchus* and possibly *V. triplicostata*. *Proterosuchus*, however, is the only taxon in this analysis known to lack laterosphenoid-postorbital contact (Clark *et al.* 1993).

20. Epipterygoid articulation. The epipterygoid articulates with the skull roof in *Proterosuchus* (Clark *et al.* 1993), but with the laterosphenoid in, for example, *Parasuchus* (Chatterjee 1978) and possibly *Erythrosuchus*. The use of this character, however, relies on the discovery of well-preserved and articulated material and in the present analysis the condition is known with certainty only for the *Parasuchia*.

21. Supraoccipital contribution to occipital peg. In erythrosuchids there is a free-standing and conical posterior peg formed by the postparietal. In *Shansisuchus* and *Vjushkovia sinensis* (DJG, pers. obs.), this peg is formed in part by the dorsal edge of the supraoccipital. The absence of *V. sinensis* in this analysis means that this feature is present only in *Shansisuchus* among the included taxa.

22. Basal tubera of the basioccipital. While Parrish (1992) was mistaken in his identification of separate lateral and ventral components to the basal tubera in a number of erythrosuchid taxa (see above), certain taxa do exhibit bilobed tubera. These include *Xilousuchus* (see above) and *Dorosuchus* (Sennikov 1989). This character is excluded because bilobed tubera are known in only a single taxon (*Xilousuchus*) included in the present analysis.

23. Presence of a medial tubercle projecting ventrally from between the basal tubera of the basioccipital. This is currently interpreted as an autapomorphy of *V. triplicostata*.

24. Anterodorsal end of the trigeminal foramen. In *Shansisuchus*, the anteriodorsal end of the trigeminal foramen appears to be narrow and extending onto the laterosphenoid. This is currently interpreted as a possible autapomorphy of *Shansisuchus*.

Problematical characters. These are deemed to be unsuitable because of poor current knowledge, variability within terminal taxa, or absence of satisfactorily definable states.

25. Fusion of opisthotic-exoccipital. The exoccipital and opisthotic are seen externally as suturally distinct elements in, for example, *Hyperodapedon* (Benton 1983), *Prolacerta* (Gow 1975; Evans 1986) and *Euparkeria* (Cruickshank 1970), but not in any of the taxa described above. The presence of fusion has been considered apomorphic for archosaurs (e.g. Benton and Clark 1988), or as having an equivocal distribution (Serenio and Arcucci 1990). It is assumed that the previous use of this character, though not explicitly defined, applies to the external, occipital surface of these elements, particularly at the base of the paroccipital process. Sutures between these elements can often be seen on the internal surface of the braincase, in or near the vestibule, even when the two elements appear to be fused in external views. Use of this character is currently hampered by the lack of descriptive information, unclear reconstructions, and ignorance about the possible ontogenetic effects. For example, Chatterjee (1974) does not describe, but reconstructs, *Paradapedon* as having a fused exoccipital-opisthotic and the condition is unclear for *Proterosuchus* based on the information presented by Gow (1975) and Cruickshank (1972). Furthermore, the use of this character may often rely on the availability of particularly well preserved material. It is here considered to currently be too poorly understood to be included in this phylogenetic analysis.

26. Anterior process of laterosphenoid. *Proterosuchus* has long and slender anterior laterosphenoid processes (Clark *et al.* 1993) and *Erythrosuchus* has short processes, while *V. triplicostata* represents something of a morphological intermediate. Information is unfortunately lacking for the laterosphenoids of a number of the earliest archosaurs, so that currently this character is of little use. Furthermore, it may be a strongly 'sliding scale' character, presenting problems for the identification of discrete character states.

27. Laterosphenoid thickness. The laterosphenoid of the earliest archosaurs is a thick bone, differing from the thin-walled homologue in, for example, modern crocodilians. This character needs further investigation based on disarticulated material, although objective recognition of discrete states might be problematical.

28. Fossae for retractor bulbi eye muscles. In all of the taxa described above, as well as in *Erythrosuchus* and *Euparkeria* (Gow 1975), the abducens foramina are positioned within a pair of fossae that are probably for the retractor bulbi eye muscles. These fossae are clearly separate from the pituitary fossa. In the archosaur outgroup taxa *Hyperodapedon* (Benton 1983), and apparently *Prolacerta* (Evans 1986), the abducens foramina lie a significant distance above the retractor fossae. This is also the condition in the extant lizard *Varanus* (Säve-Söderbergh 1946). It might be noted, however, that the abducens foramina do appear to be within the fossae in the extant taxa *Ctenosaura* (Oelrich 1956) and *Sphenodon* (Säve-Söderbergh 1946). Lack of further available information, particularly for early archosaurs, currently prevents a conclusive assessment of this character.

29. Middle cerebral vein exit. *Stagonolepis* (Walker 1990) exhibits a foramen for the exit of the middle cerebral vein that is separate to that for the trigeminal foramen. Other taxa, including *Ctenosaura* (Oelrich 1956) and *Sphenosuchus* (Walker 1990), may exhibit a partial separation of nerve and vein foramina, while most early

TABLE 1. Braincase character states for selected early archosaurs and *Prolacerta*. Characters are discussed in the text.

Taxa	Characters																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Prolacerta</i>	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0
<i>Proterosuchus</i>	0	0	0	0	0	0	0	?	?	?	0	0	1	0	0	?	?
<i>Fugusuchus</i>	0	0	?	0	0	0	0	0	?	?	0	?	1	0	0	1	2
<i>Xilousuchus</i>	0	0	1	0	0	0	1	1	1	?	0	?	0	0	0	1	2
<i>V. triplicostata</i>	0	0	1	0	0	0	1	1	1	1	0	1	0	0	0	1	2
<i>Erythrosuchus</i>	0	0	1	1	1	1	1	0	1	1	0	1	0	1	1	1	1
<i>Shansisuchus</i>	0	?	1	1	1	1	1	0	1	?	0	1	0	1	1	1	1
<i>Euparkeria</i>	0	1	0	1	0	0	1	?	?	?	0	?	1	0	0	0	0
<i>Sphenosuchus</i>	1	1	?	1	0	1	1	0	0	0	1	0	0	1	1	0	0
<i>Parasuchia</i>	1	1	0	?	0	1	?	0	1	0	1	0	?	1	1	0	1
<i>Stagonolepis</i>	1	1	?	?	0	1	1	0	?	?	1	?	?	1	1	0	?

archosaurs show no indication of any such separation. This is another character requiring further investigation and well-preserved material before a full assessment can be made. For example, *Proterosuchus* may not have a simple trigeminal foramen (Clark *et al.* 1993, fig. 2), but whether this is a real and consistent feature and/or indicative of an ossified separation of the nerve and vein is uncertain.

30. Supraoccipital. The amount of supraoccipital contribution to the border of the foramen magnum is seen to vary in archosaurs and their outgroups. For example, the supraoccipital forms some of the foramen magnum in *Paradapedon* (Chatterjee 1974), *Hyperodapedon* (Benton 1983), *Sphenosuchus* (Walker 1990), and *Parasuchia* (Chatterjee 1978), but not in any of the taxa described above. The informativeness of this character, however, is called into question by information presented by Evans (1986), who reported that *Prolacerta* is polymorphic for this character.

31. Posttemporal fenestra. This is highly reduced in *Erythrosuchus*, *Shansisuchus* and *V. triplicostata*, in which a projection on the dorsal edge of the paroccipital process articulates intimately with a concavity of the ventral surface of the parietal. *Fugusuchus* and *Proterosuchus* may lack this type of paroccipital-parietal articulation, but the posttemporal fenestra is also reduced (Cruickshank 1970, 1972; Cheng 1980). A relatively large fenestra is seen in the archosaur outgroup taxa *Prolacerta* (Gow 1975), *Paradapedon* (Chatterjee 1974) and *Hyperodapedon* (Benton 1983). There are problems with this character, both in defining discrete states and in assessing the size of the fenestra without the availability of well-preserved and articulated material. The extent of the fenestra in *Xilousuchus*, for example, is difficult to assess.

32. Slender process of the laterosphenoid. This process is a slender, ventral extension of the area separating the notches for the passage of cranial nerves II and III. To date, it has been described only in *Proterosuchus* (Clark *et al.* 1993), although it is possibly also present in *Euparkeria* (Clark *et al.* 1993).

Phylogenetic analysis

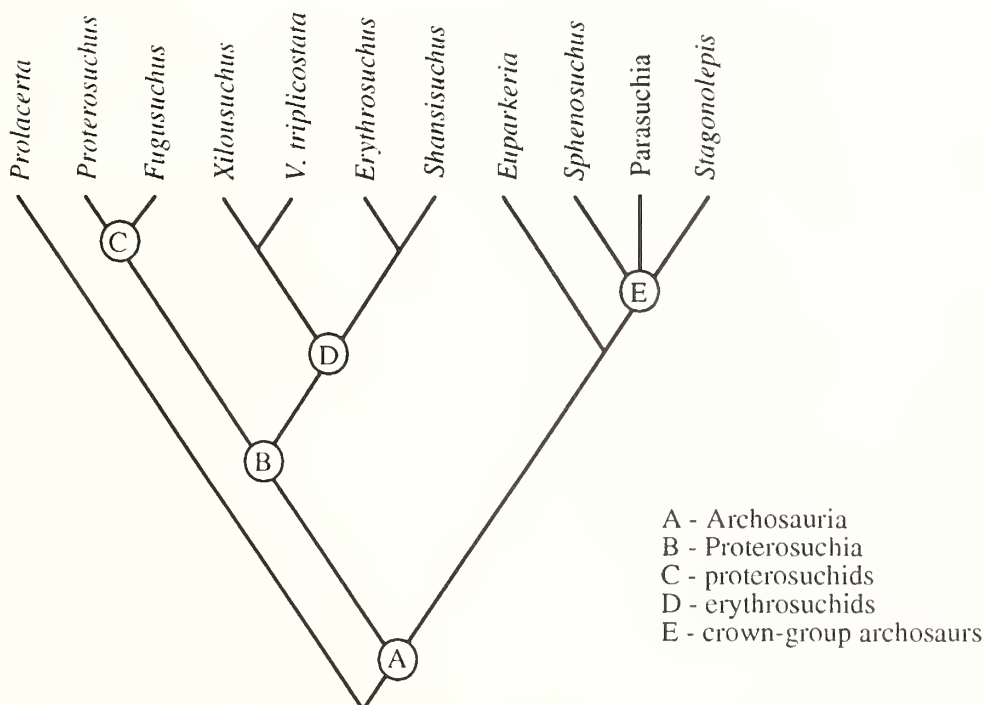
A data matrix for the 11 taxa and 17 informative characters discussed above is shown in Table 1. The data were analysed using permutation tests and parsimony.

Permutation. Two permutation tests were performed on the data as presented in Table 1. The results of permutation tests produce quantifiable measures of 'phylogenetic structure' within a given data set. The first measure applied to the data was the permutation tail probability (PTP) test (Archie 1989; Faith and Cranston 1991), a measure of the probability that a random data set would yield an equally parsimonious tree. PERMUTE (Wilkinson 1992a) was used to generate randomly permuted data sets, and to summarize the results of their analysis using Hennig86 (Farris 1988). Equal character weighting was employed and 99 random data sets were generated. This produced a result of PTP = 0.01, whether or not *Prolacerta* was included.

The second permutation test used was the character compatibility permutation tail probability (CCPTP) of Wilkinson (1992b), which is equivalent to the test statistic 'C' of Alroy (1994). This test measures the probability that a random data set would yield an equal level of character compatibility, i.e. whether or not the data set contains significant hierarchical structure (Alroy 1994). The data were analysed, with equal character weighting and 999 random data sets, using the program PICA (Wilkinson 1995). This produced a result of CCPTP = 0.0001, whether or not *Prolacerta* was included.

The results of both the parsimony-based and compatibility-based permutation tests represent the minimum possible values (given the number of random data sets employed), allowing us to reject confidently the null hypothesis that the real data do not differ significantly from random. The non-randomness is not just based on differences between the in- and outgroup, as shown by the minimum PTP and CCPTP values obtained even when *Prolacerta* was excluded. While recognizing that both of the methods used here are not without drawbacks (Alroy 1994), we conclude that these braincase data exhibit significant hierarchical structure, which is interpreted as the result of phylogeny.

Parsimony. Parsimony analysis of the data presented in Table 1 was carried out using PAUP (version 3.1.1, Swofford 1992) on a Macintosh LC computer. Searches were performed using the branch and bound option. All characters were equally weighted and unordered, and trees were rooted with the outgroup *Prolacerta*. The search yielded a single most parsimonious tree (MPT) of length (L) 26 steps with a consistency index (CI) of 0.692 and a retention index (RI) of 0.81. This tree is shown in Text-figure 7.

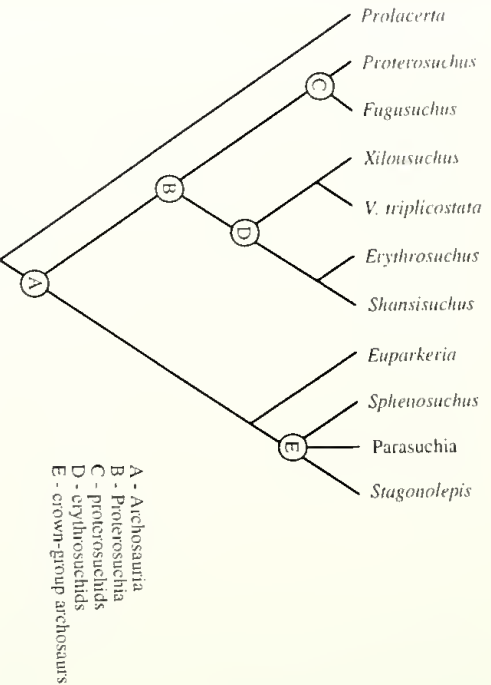


TEXT-FIG 7. Most parsimonious hypothesis of the relationships of selected early archosaurs based only on data (Table 1) from braincase morphology.

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TEXT-FIG. 7. Most parsimonious hypothesis of the relationships of selected early archosaurs based only on data (Table 1) from braincase morphology.

Prolacerta aside, there are two main clades: *Euparkeria* plus the crown-group archosaurs, and the proterosuchians. The relative position of *Euparkeria* with respect to the crown-group and proterosuchian taxa agrees with the most recent studies of archosaur phylogeny (Benton and Clark 1988; Sereno and Arcucci 1990; Sereno 1991; Parrish 1993). Two main clades can be recognized within the proterosuchians: the erythrosuchids (*Erythrosuchus*, *Shansisuchus*, *V. triplicostata*, *Xilousuchus*) and the proterosuchids (*Proterosuchus* + *Fugusuchus*). These particular hypothesized relationships are contrary to previous cladistic studies of the relationships of the earliest archosaurs (e.g. Benton and Clark 1988; Sereno 1991; Parrish 1992), all of which hypothesized that the Proterosuchia is a paraphyletic grade. The hypothesis presented in Text-figure 7 also contradicts existing views on more detailed aspects of early archosaur relationships. Recently, in the only cladistic analysis to look in any detail at the earliest archosaurs, Parrish (1992) postulated that *Fugusuchus* is an erythrosuchid rather than a proterosuchid, but the result obtained here supports Cheng's (1980) original diagnosis. *Xilousuchus*, although never before included in a cladistic analysis, was originally identified by Wu (1981) as a proterosuchid. Within the Erythrosuchidae, Parrish (1992) postulated that *Erythrosuchus* lies outside the most derived erythrosuchid clade of *Vjushkovia* + *Shansisuchus*.

The presence of the two holophyletic groups composed of *Shansisuchus* + *Erythrosuchus* and *V. triplicostata* + *Xilousuchus* (Text-fig. 7), is predictable from an examination of Table 1. *Shansisuchus* shares exactly the same character distributions as recorded for *Erythrosuchus*, except for two characters (2, 10) which are missing values for the former taxon. Because *Erythrosuchus* has no missing data in this analysis, *Shansisuchus* and *Erythrosuchus* are potential taxonomic equivalents exhibiting a 'one way asymmetrical' distribution of missing values (Wilkinson 1992b). There can, therefore, be no more parsimonious interpretation of the relationships of *Shansisuchus* than its origin from the same node as *Erythrosuchus*. A similar situation is also seen with *V. triplicostata* and *Xilousuchus*. Indeed, *Shansisuchus* and *Xilousuchus* (because they have more missing data than their respective potential equivalents) could have been safely deleted from the analysis *a priori*, without affecting the parsimonious interpretation of the relationships of the remaining taxa (Wilkinson 1992b; Wilkinson and Benton 1995). Incidentally, a character compatibility permutation test performed on the data set in Table 1 without *Shansisuchus* and *Xilousuchus* still produces minimum possible CCPTP and PTP values of 0.001 and 0.01 respectively (based on 999 and 99 random data sets respectively).

In summary, while the general structure of the cladogram in Text-figure 7 agrees with previously published analyses of basal archosaur phylogeny (*Euparkeria* is a sister group to the crown-group archosaurs; Erythrosuchidae and Proterosuchidae are holophyletic), some details are in conflict.

Additional parsimony analyses were performed with the aim of making a brief investigation of the robustness of the initial hypothesis. Various combinations of taxa presented in Table 1 were selected for re-analysis. As taxa were deleted, the number of informative characters rapidly reduced and the number of MPTs often increased. For example, excluding the crown-group archosaurs and the taxonomic equivalents *Xilousuchus* and *Shansisuchus*, left only six characters (3–4, 7, 13, 16–17) that remained informative for the six remaining taxa. PAUP analysis of this restricted data set produced five MPTs of $L = 10$; $CI = 0.7$; $RI = 0.625$. In these trees, *Proterosuchus* appears in a clade with *Euparkeria*, in a clade with *Fugusuchus*, as the sister group to *Fugusuchus* plus the erythrosuchids, as the sister group to *Euparkeria* plus the erythrosuchids and, finally, as the sister group to the erythrosuchids with *Fugusuchus* and *Euparkeria* lying outside this clade. If *Prolacerta* is subsequently removed, only four characters (3–4, 7, 13) are informative in a restricted data set including five taxa.

We investigated also the effect that the inclusion of *Prolacerta* might have on the hypothesized relationships of basal archosaurs. This was achieved by removing only *Prolacerta* from the original data set. Character 9 then became uninformative and was also removed. A PAUP analysis yielded a single MPT ($L = 23$; $CI = 0.739$; $RI = 0.838$). Lundberg rooting of this network, with the

character states observed in *Prolacerta* employed as the ancestral condition, produced the same ingroup relationships as presented in Text-figure 7. The inclusion of *Prolacerta*, therefore, does not perturb the parsimonious interpretation of relationships of the early archosaur taxa used in this analysis.

Finally, various topological constraints were employed to investigate the robustness of the relationships presented in Text-figure 7. Trees with *Fugusuchus* as a member of a holophyletic Erythrosuchidae, or with a paraphyletic Proterosuchia are only one step longer than the original MPT ($L = 27$). The shortest tree lacking a holophyletic Erythrosuchidae (*Xilousuchus* and *V. triplicostata* lying outside a clade comprising *Erythrosuchus*, *Shansisuchus* plus the crown-group archosaurs) is only two steps longer ($L = 28$).

These additional results are important in assessing the confidence we might have in the parsimonious interpretation of relationships based on braincase data. The brief investigation of restricted subsets of the original data shows that the relationships indicated in Text-figure 7 are generally supported, irrespective of the removal of some taxa and a large number of accompanying uninformative characters. The analyses performed employing topological constraints indicate that most of the relationships seen in Text-figure 7 that contradict those proposed in the recent literature (see above), are not supported in trees that are only one additional step in length. It should also be remembered that many taxa, and some characters, were excluded *a priori* because of a lack of available data. The inclusion of these data, and other cranial and postcranial characters, may significantly affect the interpretation of relationships. While raising some interesting questions that deserve further investigation, proterosuchian monophyly for example, the relationships seen in Text-figure 7 should certainly not be taken as a definitive view of early archosaur phylogeny.

Finally, we will comment briefly on the level of homoplasy in these braincase data. Parrish (1993, p. 304) has recently suggested that archosaurian braincase features may yield more informative phylogenetic data than some other cranial features obtained from taxa which share superficially similar, carnivorously adapted skulls. That braincases are relatively conservative in their evolution and less prone to convergences occurring through functional requirements, such as feeding mode, is perhaps a widely held, though rarely explicitly stated, view (though see e.g. Gow 1975, p. 118). The instability of the hypotheses discussed here, and the unremarkable CI levels obtained (seven of the 17 characters had a CI of 0.5 in the MPT), cannot be considered to support an hypothesis that archosaurian braincase morphology represents a source of especially informative phylogenetic data. However, we accept that the restricted range of taxa and methods employed here leave considerable room for further investigation.

While the levels of homoplasy in the data indicate that the early archosaur braincase is not exempt from evolutionary convergences, a closer inspection of the character state transformations required by the most parsimonious phylogenetic hypothesis raises some interesting points. Of the eight homoplastic characters, four (4, 6, 14–15) are probably best explained by the convergent acquisition of states in *Erythrosuchus* + *Shansisuchus* and non-proterosuchian archosaurs, and a further one (7) in all erythrosuchids and non-proterosuchian archosaurs. Of the remaining homoplastic characters, two (9, 17) can be considered as convergences in the pattern of sutural contact on the floor of the endocranial cavity between erythrosuchids and parasuchians, while the last (13) is the probably convergent acquisition of a constricted base to the parasphenoid rostrum in proterosuchids and *Euparkeria*. Although homoplasy is usually viewed as the bane of phylogeny reconstruction, it should be remembered that it is an over-simplification to perceive it merely as misleading evidence, particularly when a distinction between sister group and non-sister group homoplasy is made (Wilkinson 1991). For example, the four features shared by *Erythrosuchus* and *Shansisuchus* that are considered to have been acquired convergently in some non-proterosuchian archosaurs might be considered to be an important part of the evidence supporting the hypothesis that these two erythrosuchids are sister taxa, despite the homoplastic nature of these characters across the data set as a whole. It is also of interest to look at the character transformations implied by the most parsimonious hypothesis from another perspective. For example, a division of the characters into loosely defined categories reveals that those concerning the number and position of

braincase foramina (1, 3, 12, 16) show no homoplasy, while those associated with shape changes (4, 7, 13, 15) all have a CI of 0.5. We are obviously reluctant to make any sweeping conclusions based on this preliminary and rudimentary investigation of the complex question of homoplasy and character informativeness, but believe that it highlights some areas for future work that will be of interest from a functional and evolutionary perspective as well as a purely phylogenetic one.

Braincase data as a whole does not appear to be a panacea for the reconstruction of early archosaur phylogeny. Rather, we suggest that progress will be made in our understanding of both the morphology and relationships of early archosaurs by investigating all regions of the skeleton in greater detail, and by carefully exploring the phylogenetic information that their morphology may yield. The results presented here represent but a small initial step.

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APPENDIX – ABBREVIATIONS USED IN FIGURES

adc	'anterodorsal channel' of laterosphenoid	mcv	groove for middle cerebral vein
als	anterior process of laterosphenoid	mf	metotic foramen
aur	auricular (floccular) recess	ncp	notochordal pit
avc	anterior semicircular canal	nf	nutrient foramen
a.hvc	anterior part of horizontal (external) semicircular canal	no	notch
bbf	basioccipital-basisphenoid fossa	o	orbit
bf	basisphenoid fossa	oc	occipital condyle
bo	basioccipital	op	opisthotic
bpt	basipterygoid process	ope	occipital peg
bptf	basipterygoid facet	p	parietal
bs	basisphenoid	pf	postfrontal
btbo	basal tuber of basioccipital	plr	pseudolagenar recess
btbs	basal tuber of basisphenoid	plVII	route of palatine branch of facial nerve
cc	cotylar crest of laterosphenoid	popr	paroccipital process
cls	capitate process of laterosphenoid	ppt	attachment ridge for protractor pterygoidei
con	condylar 'neck'	pr	prootic
cot	channel for olfactory tract	prf	prefrontal
cp	clinoid process of basisphenoid	pvc	posteroventral process of parietal semicircular canal
crpro	crista prootica	rb	fossa for attachment of retractor bulbi eye muscles
cu	cultriform process of parasphenoid	ri	ridge
e	epipterygoid	s.	surface for articulation with...
eo	exoccipital	sg	stapedial groove
f	frontal	sl	'semilunar depression'
fm	foramen magnum	so	supraoccipital
fo	fenestra ovalis	su.	suture between...
goV	groove for the ophthalmic branch of nerve V	tc	tubercle
gr	groove	v.occ	ventral part of osseus common crus
hVII	route of hyomandibular branch of facial nerve	vrop	ventral ramus of the opisthotic
ica	foramen/groove for internal carotid artery	I–XII	cranial nerve number
itp	basisphenoid intertuberal plate		
ls	laterosphenoid		

PERMIAN CAPTORHINID REPTILES FROM THE ARGANA FORMATION, MOROCCO

by NOR-EDDINE JALIL and JEAN-MICHEL DUTUIT

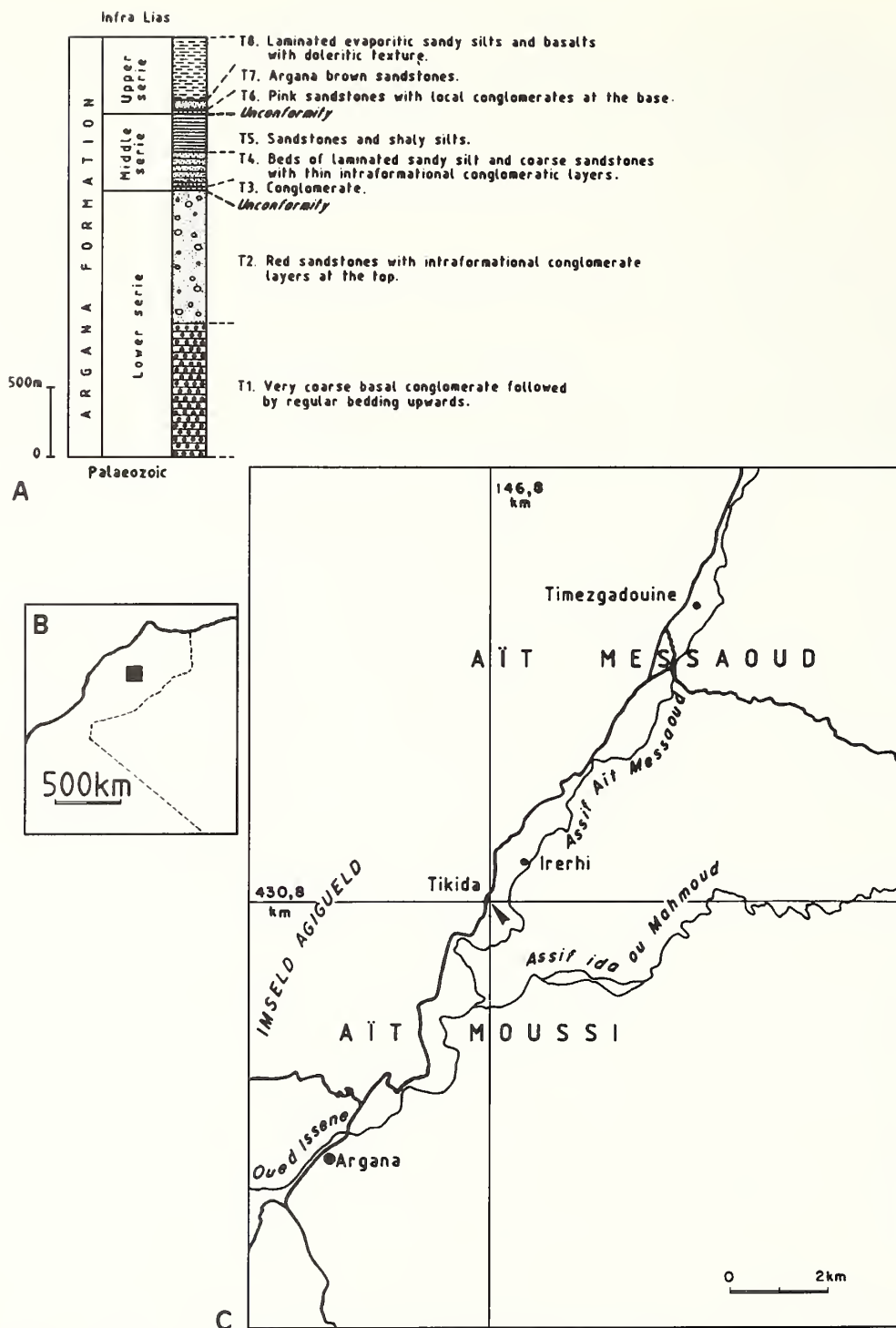
ABSTRACT. New and previously reported captorhinid material from the upper part of the Permian level T2 of the Argana Formation of Morocco is described. A maxilla bearing three tooth-rows forms the holotype of *Acrodonta irerhi*. *Acrodonta* is a medium-sized captorhinid with three rows of long and sharply pointed maxillary teeth, which differs from all other captorhinids in its acrodont tooth implantation. Dental plates and postcranial material are attributed to an unnamed member of the captorhinid subfamily Moradisaurinae. The moradisaurine remains are too poorly preserved to be attributed to either an existing or a new taxon. Nevertheless, together with *Acrodonta*, they indicate that the Captorhinidae were diverse in the Permian of North Africa. Comparison of the fauna of the upper part of Argana level T2 (diplocaulid neotridians, the captorhinid *Acrodonta* and the moradisaurine) with other faunas of Euramerica and Gondwana supports an Upper Permian age (Kazanian) for this part of the Argana Formation.

THE Argana Formation crops out in the western Upper Atlas mountains of Morocco, between Marrakech in the north and Agadir in the south (Text-fig. 1). These outcrops, known as 'Coulouir d'Argana' are 70 km long and have a maximum width of 20 km. They overlie the Palaeozoic massif of Ida-ou-Mahmoud in the east and are overlain by the Jurassic tablelands of Ida-ou-Tanan and Ida-ou-Bouzia in the west. Eight lithostratigraphical units were established by Tixeront (*in* Dutuit 1976a; Brown 1980) in the Argana Formation, namely T1–T8 (Text-fig. 1). For the lithostratigraphical data, see Brown (1980).

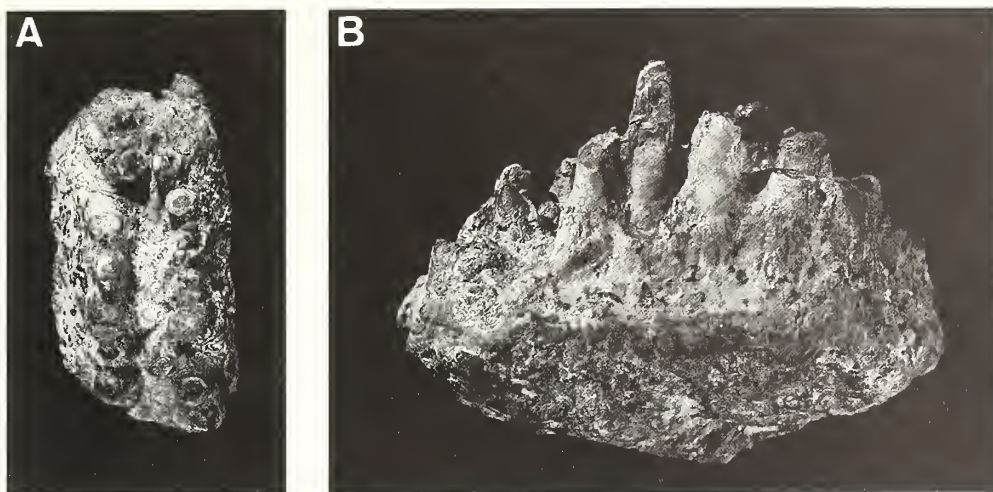
Following the first description of vertebrate remains from the Argana Formation (Arambourg and Duffaud 1960), the formation was carefully explored by Dutuit in the 1960s and 1970s. An extensive collection was made from at least 23 localities (Dutuit 1976a) and brought for study to the Laboratoire de Paléontologie of the Muséum National d'Histoire Naturelle, Paris. Most of this vertebrate material proved to be Upper Triassic and is from the levels T4 and T5 (Text-fig. 1). The pre-Triassic tetrapods are from the upper part of level T2, which is Permian. The fauna includes abundant, mostly unprepared, cranial and postcranial material of diplocaulid neotridians, (*Diplocaulus minimus*; Dutuit 1976c, 1988), and further unprepared material of large reptiles that may include synapsids (A. de Ricqlès, pers. comm.).

Dutuit (1976b) recorded three tooth-bearing bones (one maxilla and two maxillary dental plates) from the upper part of the T2 level. Working on the contemporary assumption that this level was Triassic and giving weight to the acrodont dental implantation in these specimens, he referred this material to a 'rhynchocephalian' for which he coined the name *Acrodonta irerhi*. Later, in describing the neotridian diplocaulids from the upper part of T2, he suggested instead that this material could be referred to a captorhinomorph reptile (Dutuit 1988). Further preparation of this material and its restudy in the light of recent data show that it actually belongs to two distinct captorhinid taxa including one member of the subfamily Moradisaurinae. The present study reappraises the cranial material described by Dutuit (1976b) as well as new postcranial remains from the same stratigraphical level and collected at the same time.

First known from the terrestrial deposits of Lower Permian and the lower part of the Upper Permian of USA (New Mexico, Oklahoma and Texas), the Captorhinidae have been described from the Upper Permian of Russia (Vyushkov and Chudinov 1957; Ivachnenko 1990), Niger (Taquet 1969; de Ricqlès and Taquet 1982), Zimbabwe (Gaffney and McKenna 1979), and India (Kutty 1972). Whereas the most primitive Lower Permian captorhinids were small and probably



TEXT-FIG. 1. A, stratigraphical section of the Argana Formation near Argana village. B, map of Morocco showing area of study. C, map showing the *Acrodonta irerhi* locality.



TEXT-FIG. 2. *Acrodonta irerhi* Dutuit, 1976b; holotype, ARG 506; Lower Argana Formation, Permian of Morocco; right maxilla in (A) occlusal and (B) lingual views. A, $\times 2$; B, $\times 3$.

insectivorous, the most advanced Upper Permian forms, the subfamily Moradisaurinae, show trends towards increased body size. This pattern, associated with the acquisition of multiple rows of marginal teeth, is thought to be a strong indication of herbivory and the Moradisaurinae are regarded as one of the earlier clades of tetrapod herbivores. This first record of a moradisaurine in North Africa is thus important in biogeographical studies of captorhinids and in our understanding of the development of terrestrial ecosystems.

The relationships of captorhinids within the early Amniota remain controversial (Clark and Carroll 1973; Gaffney and McKenna 1979; Gaffney 1980, 1990; Heaton and Reisz 1986; Gaffney and Meylan 1988; Gauthier *et al.* 1988; Reisz and Laurin 1991; Benton 1993; Lee 1993; Laurin and Reisz 1995). They are beyond the scope of this study, which is to consider the identity of the Moroccan captorhinids. For the purposes of this study, we follow the hypothesis of amniote phylogeny of Laurin and Reisz (1995) in which the Captorhinidae are closely related to the clade *Paleothyris* + *Diapsida*.

SYSTEMATIC PALAEOONTOLOGY

COTYLOSAURIA Cope, 1880

SAUROPSIDA Huxley, 1864

REPTILIA Laurenti, 1768

Family CAPTORHINIDAE Case, 1911

Genus ACRODONTA Dutuit 1976b

Type species. *Acrodonta irerhi* Dutuit 1976b

Diagnosis. As for the type and only species.

Acrodonta irerhi Dutuit 1976b

Text-figure 2

Holotype. ARG 506 (69.Ir.JMD of Dutuit 1976b): fragment of a right maxilla (Text-fig. 2); from scree, 200 m from Irerhi village, between Timesgadouine and Argana (Dutuit 1976a; Text-fig. 1).

Diagnosis. Medium-sized captorhinid with three rows of sharply pointed marginal teeth. It differs from all other captorhinids by its acrodont tooth implantation.

Description. ARG 506 is a fragment of a maxilla bearing three rows of marginal teeth. A pattern of scattered shallow pits is faintly visible and these may be the remains of dermal ornamentation. The absence of a well-marked ornamentation is certainly due to erosion. The specimen is badly crushed but its lateral and medial walls seem to be in their original form. A longitudinal crest runs along its lingual side (Text-fig. 2B), half-way up the preserved height, whereas its labial side is slightly convex laterally. This convexity is surmounted by a shallow depression which may correspond to the sutural area for the jugal or the lacrimal. Three parallel tooth-rows are seen in occlusal view. Only the bases of the teeth of the median row are now visible (Text-fig. 2A). The teeth are conical, long, straight and sharp. They are circular in cross section, with a pulp cavity which is large at its base but narrows towards the apex of the tooth. The tooth implantation is acrodont. The teeth are fused indistinguishably with the underlying bone (Text-fig. 2B). This character state is interpreted as an autapomorphy of *Acrodonta irerhi*. The tooth implantation in all other captorhinids is subthecodont.

Family CAPTORHINIDAE Case, 1911

Subfamily MORADISAURINAE de Ricqlès and Taquet, 1982

Gen. et sp. indet.

Plate 1; Text-figures 3–6

Material. ARG 507 (74 XXII.1.JMD of Dutuit 1976b), dental plate of right maxilla (Text-fig. 3A); ARG 508 (74.XXII.2.JMD of Dutuit 1976b), dental plate of left maxilla (Text-fig. 3B–C); ARG 504, left humerus (Text-fig. 5D); ARG 505, proximal end of a femur (Text-fig. 5E); ARG 509, two articulated caudal vertebrae (Text-fig. 5A–C); ARG 510, three articulated presacral vertebrae; ARG 511, four articulated presacral neural arches (Pl. 1); ARG 512, three articulated caudal centra; ARG 513, badly preserved pelvis (Text-fig. 6).

Locality. ARG 507 and ARG 508 are from the same stratigraphical level. They were recovered in a small basin (100 m across), from a 0.5–1 m thick sandstone bed. The post-cranial material (ARG 504–505, ARG 509–513) is from the same basin as ARG 507–508 but was found separated by a few metres from the latter. This locality, called Tikida, is situated between Argana in the south and Timezgadouine in the north (Lambert coordinates: 146.8 km East and 430.8 km North) (Text-fig. 1).

Description. *Labidosaurus* and the smaller captorhinids may be characterized by a rather large and massive head in comparison to the size of the postcranial skeleton. However, this does not necessarily apply to the larger captorhinids of the subfamily Moradisaurinae. If a large head is assumed, then the dental plates (ARG 507–508) and the post-cranial material (ARG 504–505, ARG 509–513) could be attributed to the same individual, as suggested by the taphonomic circumstances. Indeed, the dental plates and the postcranial material were collected from the same locality separated by only few metres, no other large tetrapods bones were found in this area and none of the described elements were duplicated. Moreover, the characteristics of the studied postcranial material do not contradict the systematic position suggested by the dental plates. Consequently, the dental plates and the postcranial material are attributed to the same individual here, with the reservation that the discovery of further material is needed to reinforce or falsify this association.

The similarity in size, proportions and shape of the right and left maxillary dental plates (respectively ARG 507 and 508), suggests that they belong to the same species if not the same individual, as they were found in close association (Dutuit 1976b). ARG 507 and 508 (Text-fig. 3) are larger and significantly different from ARG 506 (Text-fig. 2). The best preserved specimen (ARG 508) is 44 mm long, with a maximal width of 21 mm. The dental plate is enlarged laterally, dorsoventrally flattened and seems separated from the underlying bone (Text-fig. 3C). Its medial border is convex and overhangs the underlying bones. In *Moradisaurus* (de Ricqlès and Taquet 1982), the transition from the dental plate to the ornamented external surface of the maxilla is gradual. This seems also to be the case in ARG 508. The posteriormost part of the lateral side of ARG 508 is convex laterally, as in *Moradisaurus*, and indicates that the jugal region of the skull of this specimen was certainly rounded in shape. A lateral crest arises from the underlying bone and delimits the posterior border of the dentary plate. This well-developed crest ends abruptly, both laterally and medially. The anterior part of

EXPLANATION OF PLATE 1

Figs 1–2. Moradisaurinae gen. et sp. indet.; ARG 511; Lower Argana Formation, Permian of Morocco; four presacral neural arches in 1, dorsal and 2, lateral views. Both $\times 1$.

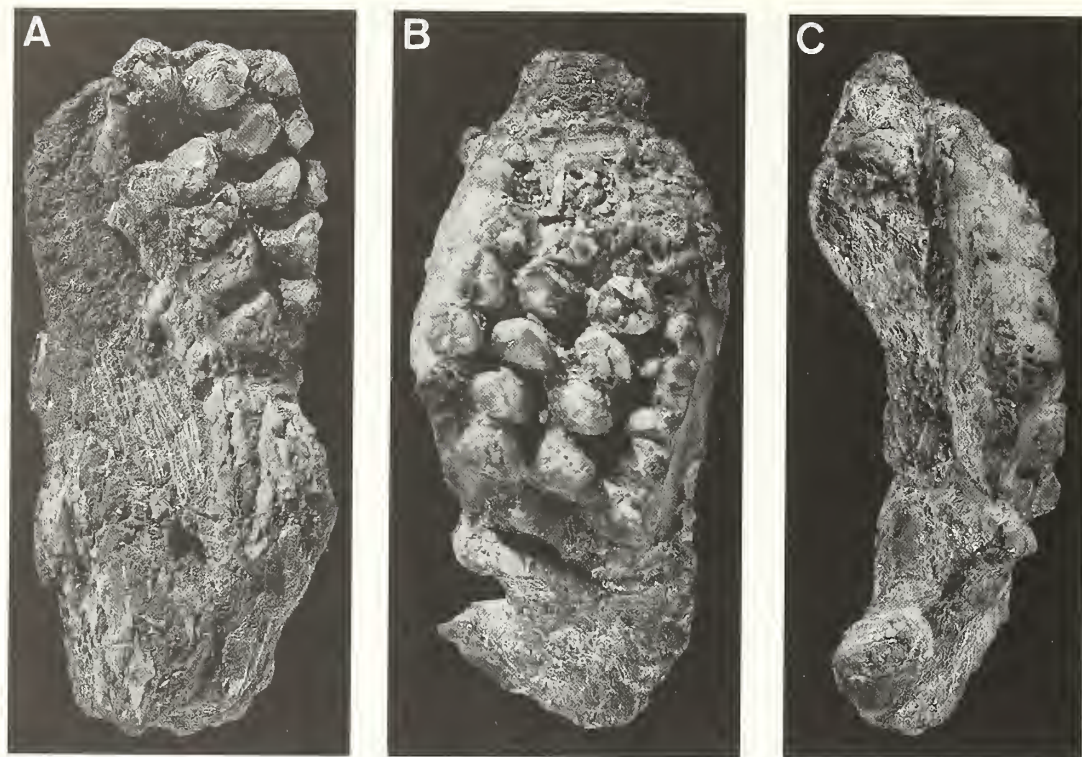
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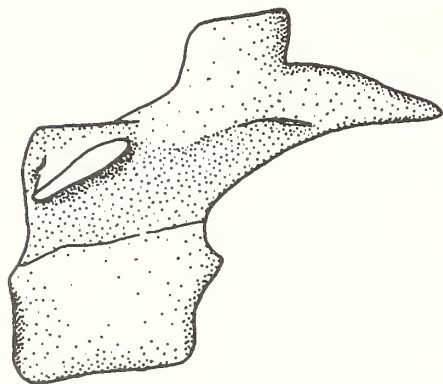
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JALIL and DUTUIT, Moradisaurinae gen. et sp. indet.

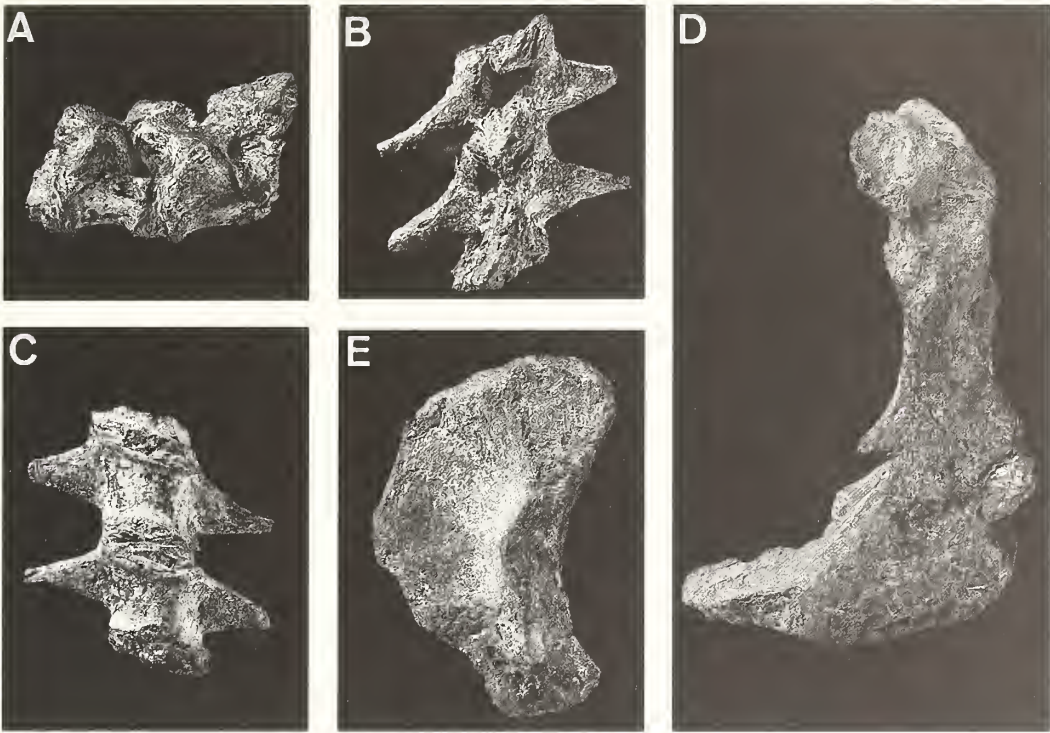


TEXT-FIG. 3. *Moradisaurinae* gen. et sp. indet.; Lower Argana Formation, Permian of Morocco. A, ARG 507, dental plate of right maxilla in occlusal view; B-C, ARG 508, dental plate of left maxilla in occlusal (B) and lingual (C) views. All $\times 2$.



TEXT-FIG. 4. *Moradisaurinae* gen. et sp. indet.; Lower Argana Formation, Permian of Morocco. Reconstruction of dorsal vertebrae in lateral view (based on ARG 510 and ARG 511). Scale bar represents 10 mm.

the dental plate is missing in both ARG 507 and ARG 508. At least four tooth rows are present on ARG 508; on ARG 507 only three rows are preserved. As in all large, multiple-tooth-rowed captorhinids, the tooth-rows are longitudinal and parallel to each other and to the lingual border. In *Captorhinus aguti*, the rows are divergent (de Ricqlès and Bolt 1983). The size and shape of all preserved teeth are similar. The teeth are conical, sub-circular in cross section and are lower and stouter than those of *Acrodonta irerhi* (ARG 506). They are slightly bulbous at the base but the apex is pointed and posteriorly recurved as shown by a well-preserved tooth, broken at its base and lying at the posteriormost part of the dental plate (Text-fig. 3B). The pulp cavity



TEXT-FIG. 5. *Moradisaurinae* gen. et sp. indet.; Lower Argana Formation, Permian of Morocco. A–C, ARG 509, two caudal vertebrae in lateral (A), dorsal (B) and ventral (C) views; D, ARG 504, left humerus; E, ARG 505, proximal extremity of a femur. All $\times 0.5$.

is large at the base of the teeth and narrows progressively towards the apex. The tooth implantation is subthecodont.

The dorsal neural arch is expanded laterally and is not completely fused to the notochordal centrum (as suggested by the isolated neural arches of ARG 511 (Pl. 1) and the longitudinal groove which separates the neural arches and the corresponding centra in ARG 510 (Text-fig. 4)). Unlike primitive reptiles, which have a centrum which is short relative to its diameter, the centra of ARG 510 are slender and are as long as high. The centra are hourglass-shaped in ventral view, with a ventral bevelling anteriorly and posteriorly for the accommodation of a large triangular intercentrum. The posterior bevelling is more pronounced, as shown by the large gap which was filled by an unpreserved intercentrum on ARG 510. There is no keel on the centrum. In ARG 510, the neural arches are noticeably swollen, but those of ARG 511 have a flat dorsal surface (Pl. 1). A swollen arch is known in all captorhinids in which the vertebrae have been studied (Dilkes and Reisz 1986; Sumida 1987, 1990). In *Labidosaurus*, the first presacral vertebrae are expanded but do not show any significant swelling (Sumida 1987, 1990). The apices of the neural spines are somewhat damaged but it is clear that they vary in height. When preserved, they are vertical and readily distinguishable from the ventrolaterally oriented surface of the neural arch (Pl. 1). A dorsal bifurcation seems to be present on the tip of the higher neural spine of ARG 511 as in *Labidosaurus* and to a lesser extent in *Captorhinus laticeps* (Dilkes and Reisz 1986, fig. 4; Sumida 1987). This bifurcation, also present in *Seymouria*, appears frequently and randomly anterior to the level of the pectoral girdle (Sumida 1987) and may have served for the attachment of supraspinal ligaments which supported the head (Dilkes and Reisz 1986). The pre- and postzygapophyses meet in a horizontal, large surface which extends laterally above the transverse process and the lateral side of the centra. A space filled by matrix separates the pre- and the postzygapophyses. This, along with the horizontal position of the zygapophyses, suggest the possibility of dorsiflexion in the vertebral column. A lateral constriction on the neural arch separates the pre- and postzygapophyses. The transverse processes project ventrolaterally and lie in the anteroventral border of the neural arch, just below the prezygapophyses (Text-fig. 4). The costal articular surfaces are badly preserved, but seem to be triangular, tapering anteroventrally.

The caudal centra (ARG 509, 512) are shorter than the dorsal centra. They are also hourglass-shaped in ventral view (Text-fig. 5). The transverse processes are well developed, and oriented posterolaterally. The neural arches are less expanded than those of the dorsal vertebrae. The neural spines are low and broad. The zygapophyses do not project laterally to the same extent as those of the dorsal vertebrae. They are tilted upwards from the horizontal plane and the articular surfaces are thus oblique.

ARG 513 is a poorly preserved pelvis (Text-fig. 6). The ilium, ischium and pubis seem to be indistinguishably fused, as in *Labidosaurus* (Sumida 1989). The ilium is lost and only its somewhat constricted base is preserved. The acetabulum is surmounted anterodorsally by a thickened bony buttress which may be interpreted as the dorsal part of the pubis. The acetabulum is hemispherical and deep. In *Captorhinus*, a large portion of the acetabulum is formed by the ilium (Fox and Bowman 1966). As in *Labidosaurus* (Sumida 1989), the fusion of the three elements of the pelvis in ARG 513 precludes direct comparisons. Anteroventral to the acetabulum is a large obturator foramen. Only the dorsal part of the ischium is preserved. It runs posteriorly from the acetabulum as a thickened ridge. The poor preservation precludes further description.

The proximal and distal heads of the humerus are orientated at 90° to one another (ARG 504, Text-fig. 5D). Its shaft is narrow by comparison to its expanded distal end. The proximal extremity is badly preserved, but seems to be less expanded than in *Captorhinus* and *Labidosaurus* (Holmes 1977; Sumida 1989). *Rhiodenticulatus* also has a more gracile humerus (Berman and Reisz 1986). A deep notch is present on the lateral border of the entepicondyle. The entepicondylar foramen was probably completely closed. The articular surfaces are not preserved on both proximal and distal ends.

Only the proximal extremity of the right femur is preserved (ARG 505; Text-fig. 5E). It is expanded (65 mm) relatively to its narrow shaft (19 mm). The internal trochanter, though incompletely preserved, appears to be well developed. It delimits a large and shallow depression, the intertrochanteric fossa. The shallowness of this depression and the thin bone in this region (6 mm) suggest that the puboischiofemoralis externus muscle was less developed than that of *Labidosaurus* (Sumida 1989) and *Rothianiscus* (Olson 1965). A bony projection is present dorsally, probably for the insertion of the puboischiofemoralis muscle (Sumida 1989).

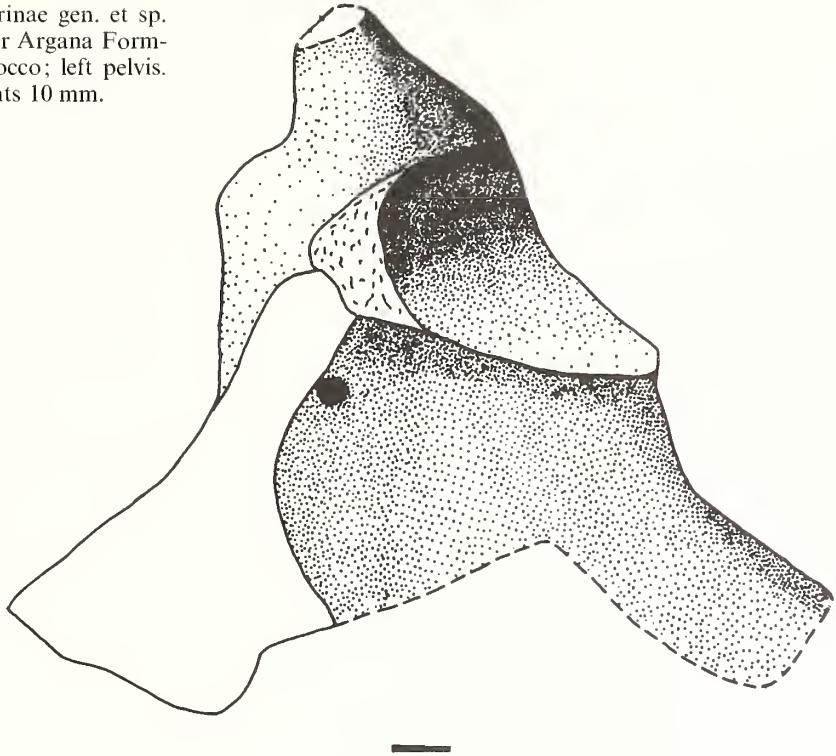
Remarks. All three tooth-bearing elements (ARG 506–508) share one derived character state which is considered to be highly diagnostic within the Captorhinidae, namely the presence of multiple rows of marginal teeth. Consequently, ARG 506–508 are attributed to the Captorhinidae. Since the Lower Permian captorhinids *Romeria* (Price 1937), *Protocaptorhinus* (Clark and Carroll 1973), *Rhiodenticulatus* (Berman and Reisz 1986), *Labidosaurus* (Cope 1896), *Captorhinus laticeps* (Heaton 1979; Gaffney 1990) and probably also the Upper Permian (Ufimian) *Riabininus* (Ivachenko 1990) have one row of marginal teeth, they are regarded as distinct from the Moroccan specimens and irrelevant to our comparison.

As described above, *Acrodonta irerhi* (ARG 506) shows character states which are significantly different from those observed on ARG 507 and 508. The smaller size, the low number of tooth-rows, the absence of an enlarged dental plate, and the size and shape of the teeth distinguish ARG 506 from ARG 507 and 508. Moreover, *Acrodonta* differs from all other captorhinids in possessing an acrodont tooth implantation. It is more primitive than *Labidosaurus*, *Captorhinus* and all other multiple tooth-rowed captorhinids in possessing sharply pointed, rather than blunt teeth, but this may be a more derived condition associated with diet.

ARG 507 and ARG 508 show more derived character-states (large size; blunt, rather than pointed, teeth; well-developed dental plate) and so fall within the Moradisaurinae of de Ricqlès and Taquet (1982) and de Ricqlès (1984), referred to as 'group 6' by Gaffney and McKenna (1979). The most noticeable postcranial characters are those of the dorsal vertebrae (slightly swollen neural arch; reduced neural spine; probably bifurcated neural spine; alternating neural spine height; large, spaced and horizontal zygapophysis).

Since first reported by Carroll (1968) in the microsaure *Pantylus*, the alternation of neural spine height has subsequently been described in such a large number of Permo-Carboniferous tetrapods (see Dilkes and Reisz 1986; Sumida 1987 for references) that its phylogenetic value is difficult to assess. More confusing is the fact that this character varies within the same family, the Captorhinidae (Heaton and Reisz 1980; Dilkes and Reisz 1986; Sumida 1987) and even in the same species, *Labidosaurus hamatus* (Sumida 1987). The bifurcation of the neural spine, which is present in *Labidosaurus*, is probably related to the presence of a massive head, as it is in the captorhinids

TEXT-FIG. 6. *Moradisaurinae* gen. et sp. indet.; ARG 513; Lower Argana Formation, Permian of Morocco; left pelvis. Scale bar represents 10 mm.



and may be a captorhinid character. Unfortunately, the vertebrae in our specimens are not sufficiently well preserved to show with certainty this character-state of the neural spine. Compared with other captorhinids, the dorsal vertebrae of ARG 510 and 511 are more similar to those of the Upper Permian moradisaurines *Kahneria* and *Rothianiscus* than they are to earlier smaller captorhinids. The neural arches are lower and broader relative to the centrum, the neural spines are lower and the zygapophyses are widely spaced and horizontal and suggest an attribution to a *Moradisaurinae*.

In recent studies on the interrelationships of captorhinids, the relationships of the basal genera have proved to be relatively uncontroversial, but the relationships of the *Moradisaurinae* (group 6 of Gaffney and McKenna 1979), have been neglected and are far from resolved. Until recently, it had been assumed that the multiple marginal tooth-rows represent a unique derived character-state within the Captorhinidae and that *Captorhinus aguti* is the primitive sister-group of all other multiple-rowed captorhinids (Gaffney and McKenna 1979; de Ricqlès and Taquet 1982; de Ricqlès 1984; Berman and Reisz 1986). Leaning on Olson's (1962) work, de Ricqlès (1984) proposed a cladogram depicting relationships of the moradisaurines. *Rothianiscus* (Olson and Beerbower 1953; Olson 1965) was linked to *Labidosaurikos* (Stovall 1950) on the basis of three character-states and together these two taxa were supposed to share one derived character-state (absence of pterygoidal teeth) with *Gecatogomphius* (Vjushkov and Chudinov 1957) and *Moradisaurus* (Taquet 1969; de Ricqlès and Taquet 1982). All the above cited genera formed an unresolved node with the other moradisaurines *Kahneria* (Olson 1962) and *Captorhinikos* (Olson 1954, 1970; Olson and Barghusen 1962).

The pterygoid is unknown in *Gecatogomphius*, and recent study has shown that small pterygoid teeth are present in *Labidosaurikos* (Dodick and Modesto 1995). Moreover, these authors have shown that *Labidosaurikos* is more closely related to the single tooth-rowed *Labidosaurus* than it is to other captorhinids, suggesting that the origin of multiple tooth-rows is diphyletic. The greatest

difficulty in studying the relationships of the Moradisaurinae lies in the fact that many taxa included in this clade are poorly known, from fragmentary material, and are distinguished from one another by their dentition or their size. All these taxa must be restudied before any phylogenetic analysis of the moradisaurines and other multiple-tooth-rowed captorhinids can be made. The Moroccan moradisaurines are too poorly preserved to be assigned confidently to an existing taxon or to be attributed to a new one and *Acrodonta* is considered as a Captorhinidae *incertae sedis*. Nevertheless, these taxa are important as indicators of the presence and the diversity of the Captorhinidae in North Africa.

STRATIGRAPHY

All the material described here was found approximately 20 m above the diplocaulid-bearing level. However, such a difference is negligible because of the thickness of the level T2 in this region of the Argana Formation. The co-occurrence of these two taxa (diplocaulid neotridians and a derived captorhinid) leads to two stratigraphical hypotheses.

1. Until now, it has been agreed that the upper part of the level T2 of the Argana Formation was Early Permian because of the presence of the diplocaulid neotridian (Dutuit 1976c, 1988; Milner 1993). This hypothesis is now weakened by two palaeontological records, namely the discovery by Olson (1972) of an Upper Permian diplocaulid, *Diplocaulus parvus*, and the discovery of the large derived captorhinids in level T2 (this study). Nevertheless, if we accept this hypothesis, the Moroccan captorhinids would be the earliest known non-North American captorhinids. Previously, the earliest record of a non-North American captorhinid was from the lower part of the Upper Permian (Ufimian, Ivachnenko 1990).

2. A scheme of the geographical and stratigraphical repartition of the captorhinids was given by de Ricqlès (1984, fig. 1). The captorhinids occur from the Lower Permian of North America (*Romeria*, Sakmarian, Texas; *Rhiodenticulatus*, Sakmarian, New Mexico; *Protocaptorhinus*, Upper Sakmarian–Lower Artinskian, Texas; *Labidosaurus*, Upper Artinskian, Texas; *Captorhinus*, Artinskian, Texas and Oklahoma; *Captorhinikos*, Kungurian, Texas and Oklahoma; *Labidosaurikos*, Kungurian, Texas and Oklahoma) to the Upper Permian (*Riabininus*, Ufimian, Tatarian, Zimbabwe; and a poorly known captorhinid from India). All the non-North American captorhinids are Late Permian (from the Ufimian to the Tatarian), the Gondwanan forms being the youngest (Upper Tatarian) (Vyushkov and Chudinov 1957; Kutty 1972; Gaffney and McKenna 1979; de Ricqlès and Taquet 1982; de Ricqlès 1984; Ivachnenko 1990). The character-states of the Moroccan captorhinids and the palaeogeographical distribution of this family rather suggest the Upper Permian. The upper part of level T2 could be correlated tentatively with the Chickasha Formation (Kazanian, Oklahoma) which yielded a large derived captorhinid (*Rothianiscus*, Olson and Barghusen 1962; Olson 1965) and a relatively small diplocaulid (Olson 1972), like level T2 of the Argana Formation. If we accept this hypothesis, *Diplocaulus minimus* is Late Permian (Kazanian) and the Moroccan captorhinid the earliest Gondwanan representative of the group.

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A REVIEW OF THE MESOZOIC OSTRACOD GENUS *PROGONOCY THERE* AND ITS CLOSE ALLIES

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ABSTRACT. The cytheracean ostracod genus *Progonocythere* and its immediate allies in the Jurassic and Cretaceous are reviewed. All known species of 12 genera are considered. Only five of these genera (*Dromacythere*, *Fastigatocythere*, *Glyptocythere*, *Majungaella*, *Progonocythere*) remain valid; the seven rejected genera are *Amicytheridea*, *Glyptogatocythere*, *Malzia*, *Novocythere*, *Strictocythere*, *Tickalaracythere* and *Zerqacythere*. We consider that the level of validity among other cytheracean groups is probably similar and that this reflects a serious decline in taxonomic standards based upon the inability of many authors to discriminate between generic and specific characters. The simple philosophy that differences of kind are generic, while those of degree are specific, seems to be largely ignored by many present day ostracod workers. We advocate that, wherever possible, the diagnoses of existing genera be expanded to embrace end-members, rather than the continual creation of so many superfluous generic taxa based on specific characters, which will eventually render the science inoperable.

UNFORTUNATELY, a very large number of ostracod genera erected in the past 25 years or so have been discriminated on the basis of what the present authors consider to be specific characters. The senior author, in preparing various families of the Cytheracea for the revision of the *Treatise on invertebrate palaeontology, Part Q, Ostracoda* of which he is coordinating author, has been struck by the very large number of monotypic, or near monotypic, genera erected on extremely flimsy evidence. Any species with the slightest morphological divergence from the norm of a genus is immediately denominated as new, notwithstanding that it may be the sole representative of that taxon. The more logical procedure, of regarding such newly discovered species as new morphological end members of an existing plexus of species is rarely adopted. Some of the prolific creators of such spurious taxa are possibly of the opinion that the original diagnosis of a genus is sacrosanct and immutable when, in fact, it must inevitably be expanded as new species are encountered. In the production of the *Treatise* revision, a large number of new, ornate podocopid genera of various families have been subsumed as junior synonyms within pre-existing genera by the simple and logical expedient of emending the diagnosis of pre-existing genera.

It is almost always taxa with prominent ornamentation which are associated with this form of generic 'splitting'. Smooth ostracods, always difficult to deal with taxonomically, are much more stable generically. In many cases, it seems that authors do not understand the differences between what are primary and secondary aspects of ostracod ornament. For example, if ten or so species of a genus all have the same primary ornament, (say) of three parallel ribs, then to encounter a species similar in all other respects but with only two ribs or with four, is possibly to have found something worthy of separate generic status. However, if all of those ten species are, in their intercostal areas, differently ornamented (this being a secondary feature), these differences are important specific characters and no more. All too often, authors have used such secondary ornamentation to create new genera and complicate, almost beyond function, the existing taxonomic system. One needs only to look at the near total anarchy which exists in the Foraminiferida, with hundreds of monotypic genera, to know that this is a practice which should be suppressed.

To work in taxonomy is to exercise judgement and not to try to break records. If authors were to apply the philosophy that differences of kind were generic, while those of degree were specific, then a much more rational system would prevail.

In the following study, we examine 12 Mesozoic podocopinid cytheracean ostracod genera of the family Progonocytheridae Sylvester-Bradley, most closely related in their morphology to the genus *Progonocythere* Sylvester-Bradley (Table 1). We find that seven are readily referable to other genera

TABLE 1. The twelve genera of Progonocytheridae considered here, arranged in date order, with type species and geographical distribution. The five genera considered to be valid are in *italics*.

Genus	Author and date	Type species	Stratigraphical and geographical distribution. New distributions resulting from this review in bold
<i>Progonocythere</i>	Sylvester-Bradley, 1948	<i>P. stilla</i>	Bajocian–Oxfordian: Britain, Europe, Israel, Egypt, Saudi Arabia, India, Madagascar; L. Bajocian: Australia
<i>Glyptocythere</i>	Brand and Malz, 1962	<i>G. tuberodentina</i>	Bajocian–Bathonian: Britain, Europe
<i>Majungaella</i>	Grekoff, 1963	<i>M. perforata</i>	Callovian–Maastrichtian: East and South Africa, Madagascar, India, Australia, S. Chile , Argentina, Falkland Plateau, E. Brazil
Malzia	Bate, 1965	<i>M. bicarinata</i>	Bajocian: Britain
<i>Fastigatocythere</i>	Wienholz, 1967	<i>F. rugosa</i>	Bathonian–Kimmeridgian: Britain, Europe, Egypt, Jordan, Saudi Arabia, East and South Africa, Madagascar, India; Lower Bajocian: Australia
Novocythere	Rossi de García, 1972	<i>N. santacruziana</i>	Aptian–Albian: Argentina
Amicytheridea	Bate, 1975	<i>Procytheridea thopyensis</i>	Bajocian–Callovian: Saudi Arabia, East Africa
Tickalaracythere	Krömmelbein, 1975	<i>T. ticka</i>	Campanian–Maastrichtian: east Brazil; Albian–Campanian: Australia
Glyptogatocythere	Basha, 1980	<i>G. malzi</i>	Bathonian: Jordan; Bajocian–Bathonian: Egypt
Zerqacythere	Basha, 1980	<i>Z. subiehiensis</i>	Bathonian: Jordan, Egypt, Saudi Arabia
<i>Dromacythere</i>	Ware and Whatley, 1980	<i>D. sagittata</i>	Upper Bathonian: Britain
Strictocythere	Sheppard in Brand, 1990	<i>Progonocythere polonica</i>	Upper Bathonian: Britain, Europe; Lower Bajocian: Australia

within the complex and that only five are valid. This, of course, is a matter of judgement. However, we have in the course of this study, examined and considered all of the species attributed to each of the original 12 genera. Sad to relate, in many areas of the *Treatise* revision, approximately the same percentage of validity seems to obtain!

THE GENERA

In the *Treatise* revision, the Progonocytheridae will comprise only genera with entomodont/lobodont hinges (*sensu* Moore and Pitrat 1961; *non* Van Morkhoven 1962). The family will be divided into the Progonocytherinae, comprising subovate to subtriangular genera with a convex

dorsal margin and more or less strong ventro-lateral tumidity, similar to those discussed here, and another subfamily which will embrace subrectangular to subquadrate genera. The latter group comprises such genera as *Acanthocythere* Sylvester-Bradley, 1956, *Afrocytheridea* Bate, 1975, *Lophocythere* Sylvester-Bradley, 1948, *Neurocythere* Whatley, 1970, *Terquemula* Blaszyk and Malz, 1965, and *Trichordis* Grekoff, 1963. These are the subject of a subsequent review by the authors which is in preparation.

In order to facilitate comparison between them, the most important morphological characters of the 12 genera included in the present study, are outlined in Table 2; those which we consider to be valid are in italics.

Progonocythere Sylvester Bradley, 1948

This genus was based initially on three species: *Cythere blakeana* Jones, 1884, *C. juglandica* Jones, 1884 and *Progonocythere stilla*, the last named being a new species chosen by Sylvester-Bradley as the type. All these species had the 'hinge characteristics of the subfamily': a straight hinge composed of three elements, anterior, posterior and median, in which the median element is further subdivided into antero-median and postero-median parts. In the larger (left) valve, the anterior and posterior elements are short, loculate sockets; the median element is a bar, the anterior portion of which is always dentate, the posterior portion being denticulate. In the smaller (right) valve, the anterior and posterior elements are short dentate bars, the anterior always, the posterior usually, denticulate. The median element is clearly divided into an expanded anterior groove with four or five distinct loculi, and a posterior groove narrower than the anterior, with more numerous but less clearly defined locellae. The above description of the entomodont hinge is modified from Sylvester-Bradley (1948, p. 189).

Whatley (1964) reviewed the status of the genus and indicated that some species added since 1948 were better accommodated elsewhere. Forms with antimerodont rather than entomodont hinges in particular were excluded. Some of the species rejected from the genus by Whatley (1964) have subsequently been described as new genera, e.g. *Progonocythere hieroglyphica* Swain and Peterson is now assigned to *Pseudoperissocytheridea* Mandelstam (see Whatley 1970, p. 351).

In the present review, we have encountered numerous species placed in *Progonocythere*, mostly since 1964, which we consider would be best removed from the genus and accommodated elsewhere. These are listed below (in date order of first citation of combination) together with two of Sylvester-Bradley's (1948) original three species which have been transferred since 1964.

1. *Progonocythere juglandica* (Jones, 1884) in Sylvester-Bradley 1948 (pl. 12, figs 5–6), from the Middle Jurassic of Europe and Madagascar was assigned to *Fastigatocythere* by Wienholz (1967).
2. *Progonocythere blakeana* (Jones, 1884) in Sylvester-Bradley 1948 (pl. 12, figs 3–4), from the Middle Jurassic of Europe, is assigned to *Terquemula* Blaszyk and Malz following Bate (1969, p. 393) who designated, discussed and illustrated the lectotype.
3. *Progonocythere caswellensis* Brown, 1957 (in Catalogue of Ostracoda 1952, figs 14–15), from the Upper Cretaceous of North Carolina, should be included in *Pseudoperissocytheridea* Mandelstam because of its antimerodont hinge and ornament.
4. *Progonocythere? bemelenensis* (Veen) and *Progonocythere subcarinata* (Bosquet) in Howe and Laurencich 1958, p. 470, from the Maastrichtian of South Limburg, Holland, are both *Brachycythere* Alexander.
5. *Progonocythere* sp. A Wall, 1960 (pl. 28, figs 12–14), from the Callovian of Saskatchewan, Canada, resembles *Glyptocythere* Brand and Malz, but its hinge is antimerodont and it should be removed from the Progonocytheridae.
6. *Progonocythere juglandica* (Jones) subsp. *malgachica* Grekoff, 1963 (pl. 3, figs 56–62; pl. 8, fig. 216), *P. accessa* Grekoff, 1963 (pl. 3, figs 63–68), *P. bicrucata* Grekoff, 1963 (pl. 3, figs 69–76; pl. 8, figs 218–221), *P. befotakaensis* Grekoff, 1963 (pl. 3, figs 77–80; pl. 8, figs 215, 217) and *Progonocythere* 2393 Grekoff, 1963 (pl. 4, figs 105–108), all from the Bathonian and Callovian of Madagascar, were assigned by Wienholz (1967) to *Fastigatocythere*.

TABLE 2. The 12 genera of Progonocytherinae considered here, giving author, date of publication, number of species and details of size and most important morphological characters. Valid taxa are written in bold.

Genus	Size mm	Shape	Ornament	Muscle scars	Hinge	Anterior rpe	Eye tubercle
<i>Progonocythere</i> Sylvester-Bradley, 1948 Approximately 27 spp.	Mean L. 0.65, H. 0.38, W. 0.28, Range L. 0.45-0.85, H. 0.28-0.49, W. 0.14-0.42	Ovate, subovate, subrectangular, subquadrate ventro-laterally, tumid	Smooth, punctate, pitted, weakly reticulate, ventral longitudinal ribs, some shallow med. sulcus	Vertical/curved 4 adductors single heart-shaped/oval frontal single mandibular, some ? 2	Entomodont. Accommodation groove LV some spp.	Straight, well spaced usually 8, ranges to 16. Avestibulate	Eye-swelling and post-ocular sulcus in some species
<i>Glyptocythere</i> Brand and Malz, 1962 Approximately 40 spp.	Mean L. 0.87, H. 0.37, W. 0.32, Range L. 0.50-1.25, H. 0.32-0.43, W. 0.22-0.42	Egg-shaped to trapezoidal, laterally inflated, dorsal of LV arched	With or without strong reticulation with separate longitudinal and vertical ribs or low swellings	Curved/vertical 4 adductors one frontal and one mandibular scar	Strong entomodont	Straight, well spaced 9-12. Avestibulate	Absent
<i>Majungarella</i> Grekoff, 1963 Approximately 20 spp.	Mean L. 0.70, H. 0.46, W. 0.46, Range L. 0.73-0.98, H. 0.30-0.62, W. 0.39-0.53	Subtriangular to pyriforme, upturned posterodorsally, strongly inflated/dorsal view	Coarse punctae radiating in rows from dorsal margin then concentric. Ventral ribs. Anterior denticles	Vertical/oblique 4 adductors, single circular frontal scar and one oval mandibular	Entomodont	Originally curved and 14-20. Now up to 28. Some narrow vestib.	Eye tubercle and post-ocular sulcus
<i>Malzia</i> Bate, 1965 2 spp.	Mean L. 0.77, H. 0.44, W. 0.41, Range L. 0.69-0.85, H. 0.43-0.45, W. 0.38-0.44	Subquadrate, tapering to posterior margin	Smooth or punctate. Ventro- lateral part extended into 1 or 2 keel-like projections	Curved row of 4 adductors round anterior-dorsal antennal scar. Mandibular scar not seen	Entomodont. Narrow, elongate, accommodation groove LV	Long, straight, well spaced. Approx. 8	Low eye tubercle. Not seen in all illustrated specimens
<i>Fastigatocythere</i> Weinholz, 1967 Approximately 12 spp.	Mean L. 0.68, H. 0.37, W. 0.78, Range L. 0.43-0.93, H. 0.25-0.50, W. 0.45-0.52	Subtriangular to subrectangular	Dorso-lateral with subvertical or inverted chevron ribs	Vertical row of 4 adductor scars and a rounded antennal scar. One mandibular scar	Entomodont	Well spaced, straight, ranging from 7-9	Eye tubercle and marked post- ocular sulcus

<i>Novocythere</i> Rossi de Garcia, 1972 1 sp.	Mean L. 0.90, W. 0.57, Range L. 0.85-0.95, W. 0.55-0.60	Pyriiform, upturned postero-dorsally, strongly convex in dorsal view	Concentric puncta. Anterior and posterior marginal denticles	Curved row of round and approximate adductor scars	Entomodont	Approximately 25	Low, elongate eye swelling
<i>Amicytheridea</i> Bate, 1975 5 spp.	Mean L. 0.60, H. 0.36, W. 0.35, Range L. 0.55-0.65, H. 0.35-0.37, W. 0.33-0.37	Subtriangular	Dorso-lateral ribs inverted chevron not projecting above dm. Ventro-lateral ribs parallel to venter	Curved row of 4 adductors with an antero-central frontal scar	Lobodont	Straight to slightly curved antero- ventrally. Approx. 14	Eye tubercle and post-ocular sulcus
<i>Tickalaracythere</i> Krömmelbein, 1976 3 spp.	Mean L. 1.04, H. 0.67, Range L. 0.92-1.17, H. 0.58-0.76	Trapezoidal, pyriiform, upturned postero- dorsally. Strongly convex dorsal view	Coarsely punctate with rows diverging from the dorsal margin. Anterior marginal denticles	Row of 4 adductors, antennal scar heart- to V-shaped, one mandibular	Entomodont	Straight to slightly curved, 24-28	Eye-tubercle and post-ocular sulcus
<i>Glyptogatoacythere</i> Basha, 1980 2 spp.	Mean L. 0.69, H. 0.49, W. 0.37, Range L. 0.62-0.76, H. 0.37-0.45, W. 0.35-0.40	Subtriangular, ovate, centrally tumid, somewhat pointed laterally in dorsal view	Subtriangular ribs in inverted chevron	No data	Entomodont	No data	Eye tubercle and marked post- ocular sulcus
<i>Zerqacythere</i> Basha, 1980 2 spp.	Mean L. 0.60, H. 0.33, W. 0.32, Range L. 0.55-0.67, H. 0.30-0.37, W. 0.30-0.35	Subtriangular	Subtriangular ribs in inverted chevron which do not overreach dm. and broken by large tubercles	No data	Entomodont	No data	Eye tubercle and marked post- ocular sulcus
<i>Dromacythere</i> Ware and Whatley, 1980 1 sp.	Mean L. 0.44, H. 0.25, W. 0.25, Range L. 0.41-0.48, H. 0.20-0.24, W. 0.25	Subquadrate to globose, dorsally umbonate, ventro-laterally tumid	Reticulate	4 subvertical rounded-oval adductors, rounded antennal, ? divided mandibular scar	Strong entomodont	Straight, thick, well spaced. Approx. 8	Prominent eye tubercle and post- ocular sulcus
<i>Strictocythere</i> Sheppard in Brand, 1990 2 spp.	Mean L. 0.54, H. 0.28, W. 0.23, Range L. 0.49-0.68, H. 0.20-0.36, W. 0.22-0.24	Elongate oval, ventrolateral border slightly overhangs ventral margin	Pitted	No data	Entomodont	No data	Absent?

TABLE 2. The 12 genera of Progonocytherinae considered here, giving author, date of publication, number of species and details of size and most important morphological characters. Valid taxa are written in bold.

Genus	Size mm	Shape	Ornament	Muscle scars	Hinge	Anterior rpe	Eye tubercle
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<i>Glyptocythere</i> Brand and Malz, 1962 Approximately 40 spp	Mean L 0.87, H 0.37, W 0.32, Range L 0.50-1.25, H 0.32-0.43, W 0.22-0.42	Egg-shaped to trapezoidal, laterally inflated, dorsal of LV arched	With or without strong reticulation with separate longitudinal and vertical ribs or low swellings	Curved/vertical 4 adductors one frontal and one mandibular scar	Strong entomodont	Straight, well spaced 9-12 Avestibulate	Absent
<i>Majunguella</i> Gickoff, 1963 Approximately 20 spp	Mean L 0.70, H 0.46, W 0.46, Range L 0.73-0.98, H 0.30-0.62, W 0.39-0.53	Subtriangular to pyriforme, upturned posterodorsally, strongly inflated/dorsal view	Coarse punctae radiating in rows from dorsal margin then concentric Ventral ribs Anterior denticles	Vertical/oblique 4 adductors, single circular frontal scar and one oval mandibular	Entomodont	Originally curved and 14-20 Now up to 28 Some narrow vestib	Eye tubercle and post-ocular sulcus
<i>Malzia</i> Bate, 1965 2 spp	Mean L 0.77, H 0.44, W 0.41, Range L 0.69-0.85, H 0.43-0.45, W 0.38-0.44	Subquadrate, tapering to posterior margin	Smooth or punctate. Vento- lateral part extended into 1 or 2 keel-like projections	Curved row of 4 adductors round anterior-dorsal antennal scar Mandibular scar not seen	Entomodont. Narrow, elongate, accommodation groove LV	Long, straight, well spaced Approx 8	Low eye tubercle Not seen in all illustrated specimens
<i>Fusigatocythere</i> Weinholz, 1967 Approximately 12 spp	Mean L 0.68, H 0.37, W 0.78, Range L 0.43-0.93, H 0.25-0.50, W 0.45-0.52	Subtriangular to subrectangular	Dorso-lateral with subventral or inverted chevron ribs	Vertical row of 4 adductor scars and a rounded antennal scar One mandibular scar	Entomodont	Well spaced, straight, ranging from 7-9	Eye tubercle and marked post- ocular sulcus
<i>Novocythere</i> Rossi de Gaciva, 1972 1 sp	Mean L 0.90, W 0.57, Range L 0.85-0.95, W 0.55-0.60	Pyriform, upturned postero-dorsally, strongly convex in dorsal view	Concentric puncta Anterior and posterior marginal denticles	Curved row of round and approximate adductor scars	Entomodont	Approximately 25	Low, elongate eye swelling
<i>Anticytheridea</i> Bate, 1975 5 spp	Mean L 0.60, H 0.36, W 0.35, Range L 0.55-0.65, H 0.35-0.37, W 0.33-0.37	Subtriangular	Dorso-lateral ribs inverted chevron not projecting above dm Vento-lateral ribs parallel to venter	Curved row of 4 adductors with an anterocentral frontal scar	Lobodont	Straight to slightly curved antero- ventrally Approx. 14	Eye tubercle and post-ocular sulcus
<i>Tickalarocythere</i> Krommelbein, 1976 3 spp	Mean L 1.04, H 0.67, Range L 0.92-1.17, H 0.58-0.76	Trapezoidal, pyriform, upturned postero- dorsally Strongly convex dorsal view	Coarsely punctate with rows diverging from the dorsal margin Anterior marginal denticles	Row of 4 adductors, antennal scar heart- to V-shaped, one mandibular	Entomodont	Straight to slightly curved, 24-28	Eye tubercle and post-ocular sulcus
<i>Glyptogatocythere</i> Basha, 1980 2 spp	Mean L 0.69, H 0.49, W 0.37, Range L 0.62-0.76, H 0.37-0.45, W 0.35-0.40	Subtriangular, ovate, centrally tund, somewhat pointed laterally in dorsal view	Subtriangular ribs in inverted chevron	No data	Entomodont	No data	Eye tubercle and marked post- ocular sulcus
<i>Zenagocythere</i> Basha, 1980 2 spp	Mean L 0.60, H 0.33, W 0.32, Range L 0.55-0.67, H 0.30-0.37, W 0.30-0.35	Subtriangular	Subtriangular ribs in inverted chevron which do not overreach dm and broken by large tubercles	No data	Entomodont	No data	Eye tubercle and marked post- ocular sulcus
<i>Dromacythere</i> Ware and Whatley, 1980 1 sp	Mean L 0.44, H 0.25, W 0.25, Range L 0.41-0.48, H 0.20-0.24, W 0.25	Subquadrate to globose, dorsally umbonate, ventro-laterally tund	Reticulate	4 subvertical rounded oval adductors, rounded antennal, ? divided mandibular scar	Strong entomodont	Straight, thick, well spaced. Approx 8	Prominent eye tubercle and post- ocular sulcus
<i>Strictocythere</i> Sheppard in Brand, 1990 2 spp	Mean L 0.54, H 0.28, W 0.23, Range L 0.49-0.68, H 0.20-0.36, W 0.22-0.24	Elongate oval, ventrolateral border slightly overhangs ventral margin	Pitted	No data	Entomodont	No data	Absent?

7. *Progonocythere falcata* Grekoff, 1963 (pl. 4, figs 88–91), from the Middle Callovian of Madagascar, probably belongs in *Fastigatocythere* Wienholz because of its triangular and posteriorly acuminate shape and post-ocular sulcus.
8. *Progonocythere mundula* Grekoff, 1963 (pl. 4, figs 92–95), from the Middle Callovian of Madagascar, certainly belongs in *Majungaella* Grekoff.
9. *Progonocythere? juglandica* (Jones) *sensu* Oertli 1963 (pl. 28, fig. 2b), from the Bathonian of France, certainly belongs in *Fastigatocythere* Wienholz.
10. *Progonocythere? aff. anoda* Peterson subsp. *ancestor* (Oertli) *in* Maync, 1966 (pl. 10, fig. 48), from the Bathonian of Israel, belongs in *Fastigatocythere* Wienholz (= *F. bakeri* (Basha) *sensu* Rosenfeld *et al.* (1987, pl. 3, figs 1–8)).
11. *Progonocythere? posteriohumulus* Blaszyk, 1967 (pl. 20, figs 11–13; text-fig. 20) from the Middle Bathonian of Poland, seems to have an antimerodont hinge and is much too elongate-acuminate posteriorly to be *Progonocythere*. In shape, it resembles *Aalenella* Plumhoff.
12. *Progonocythere (Majungaella) nematis* Dingle *in* Dingle and Klinger, 1972 (pl. 18, fig. a), from the Upper Jurassic of South Africa, belongs in *Majungaella* Grekoff.
13. *Progonocythere (Majungaella) brentonensis* Dingle *in* Dingle and Klinger, 1972 (fig. 4; pl. 16, figs f–i; pl. 17, figs a–c), from the Upper Jurassic of South Africa, belongs in neither *Progonocythere* nor *Majungaella*, which we regard as discrete taxa. This species belongs in *Fastigatocythere* Wienholz, because of its triangular and posteriorly acuminate shape, its post-ocular sulcus and (although weakly developed) its inverted chevron ornament.
14. *Progonocythere (Majungaella) reticulata* Dingle *in* Dingle and Klinger, 1972 (pl. 17, figs d–i) (*non Progonocythere reticulata* Bate, 1963 which is a true *Progonocythere*) is from the Upper Jurassic of South Africa. From its shape and outline, we consider it to belong in *Afrocytheridea* Bate.
15. *Progonocythere spitiensis* Jain and Mannikeri, 1975 (pl. 1, figs f–h), from the Upper Jurassic of India, certainly belongs in *Majungaella* Grekoff.
16. *Progonocythere befotkaensis (sic)* Grekoff *sensu* Guha (1976, pl. 2, figs 12a–b, 13), from the Upper Jurassic of Kutch, India, belongs in *Fastigatocythere* Wienholz.
17. *Progonocythere plettenbergensis* McLachlan, Brenner and McMillan, 1976 (pl. 16, figs 3–7), from the Hauterivian of well PB-A/1 (South Africa), belongs in *Fastigatocythere* Wienholz.
18. ? *Progonocythere* sp. A McLachlan *et al.*, 1976 (pl. 16, figs 8–10), from the ?Berriasian–Lower Valanginian of well PB-A/1 (South Africa), belongs in *Fastigatocythere* Weinholz.
19. *Progonocythere reticulata* Dingle *in* McLachlan *et al.*, 1976 (pl. 16, figs 1–2), from the Valanginian of well PB-A/1 (South Africa), should be included in *Afrocytheridea* Bate.
20. *Progonocythere brentonensis* Dingle *in* McLachlan *et al.*, 1976 (pl. 15, figs 18–21), from the Valanginian of PB-A/1 well (South Africa), belongs in *Fastigatocythere* Wienholz.
21. *Progonocythere neuquenensis* Musacchio, 1978 (pl. 2, figs 14–18), from the Middle Callovian of Argentina, could, by its shape and outline, be tentatively included in *Fastigatocythere* Wienholz.
22. *Progonocythere cf. reticulata* Dingle *sensu* Musacchio, 1981 (pl. 2, fig. 12), from the Valanginian of Argentina, is similar to and possibly conspecific with Dingle's species above and is, therefore, considered to belong in *Afrocytheridea* Bate.
23. *Progonocythere pyramida*, *P. ramosa* and *P. schuleridiformis* Wasfi, El Sweify and Abdelmalik, 1982 (pl. 5, respectively figs 54–55, figs 46–48 and fig. 37), from the Bathonian and Callovian of the Gulf of Suez, Egypt, do not belong in *Progonocythere* but are placed, tentatively (due to poor descriptions and illustrations) in *Fastigatocythere* Weinholz (*pyramida*, *ramosa*) and *Galliaecytheridea* Oertli (*schuleridiformis*).
24. *Progonocythere* A Kielbowicz *et al.*, 1983 (pl. 6, fig. 12) is from the Valanginian of the Argentine part of the Austral Basin (southern Argentina). According to the illustrations (there is no description), it does not belong to *Progonocythere*; its clearly triangular outline and strong ventral rib suggest that it should be tentatively included in *Fastigatocythere* Wienholz.
25. *Progonocythere? freudni* Rosenfeld and Raab, 1984 (pl. 9, figs 10–16), from the Neocomian of Israel, is much too elongate and acuminate posteriorly. It also has a chevron-type ornament which is not typical of *Progonocythere*, and could possibly be included in *Neocythere* Mertens.
26. *Progonocythere implicata* Ljubimova and Mohan *in* Kulshreshtha *et al.*, 1985 (fig. 7.11–7.12), from the Callovian–Oxfordian of India, more closely resembles *Afrocytheridea* Bate.
27. *Progonocythere banniensis* Neale and Singh, 1985 (pl. 3, fig. 2), from the Callovian of India, more closely resembles *Afrocytheridea* Bate.

Doubtful species of Progonocythere. *Progonocythere retusa* Grekoff, 1963, from the Middle

Bathonian of Madagascar, has, according to the author, chevron-type ornament. Since this feature is not visible in the illustrations (pl. 3, figs 81–87) and the lateral surface is smooth with isolated punctation, we have provisionally retained this species in *Progonocythere* despite the fact that it is rather elongate, although not so elongate as species such as *P. polonica* Blaszyk.

Progonocythere cf. *letruelensis* (Rohr, 1976) in Malz *et al.* 1985 (pl. 6, fig. 57), from the Bajocian–Callovian of Sardinia, seems to be too strongly tumid to belong in *Progonocythere*; it may belong in *Klieana* Martin.

Progonocythere sp. Rosenfeld *et al.* 1987 (pl. 3, fig. 11), from the Oxfordian of Israel and *Progonocythere kutchiensis* Guha, 1976 (pl. 1, figs 2a–b, 3), from the Upper Jurassic of India, are doubtful species due to their incomplete description and poor illustration.

Synonymized genera. We consider that the genus *Malzia* Bate, 1965 (p. 110, pl. 9, figs 5–8; pl. 10, figs 1–3), from the British Bajocian, is merely *Progonocythere* with a ventro-lateral keel-like prolongation, similar to that of *Progonocythere yonsnabensis* Bate, 1965 (pl. 12, figs 5–14; pl. 13, figs 1–4) from the Bajocian of the Grey Limestone Series [= Scarborough Formation], Yorkshire. Similarly, we regard *Strictocythere* Sheppard in Brand, 1990 (p. 207, pl. 13, figs 8–15), from the Upper Bathonian of Europe, as merely a more elongate-oval *Progonocythere*. We have emended the diagnosis of *Progonocythere* to include the species of these synonymized genera.

Emended diagnosis of Progonocythere Sylvester-Bradley, 1948. Progonocytherinae with ovate to elongate-ovate, subrectangular or subquadrate shape; ventro-laterally tumid; with or without ventro-lateral keel-like prolongations extending below the ventral surface; smooth, punctate to pitted and weakly reticulate; ventral surface with longitudinal ribs, often shallow vertical median sulcus. Eye swelling and post-ocular sulcus present in some species. Entomodont hinge with accommodation groove in left valve in some species. Anterior pore canals usually eight but ranging to 16. Muscle scars comprising vertical or curved row of four adductors and heart or oval shaped frontal scar; usually one mandibular but two reported for some species. Left valve larger than right. Sexually dimorphic; males longer, less high and less tumid than females.

Distribution. *Progonocythere* ranges from the Bajocian to Oxfordian, although Bate (1977, p. 234) cited a species from the Kimmeridgian of Spain. It has a geographical range largely restricted to the Northern Hemisphere, particularly Britain and Europe. Ascoli (1988, p. 25) recorded, but did not illustrate, *P. polonica* and *P. aff. rugosa* from the Bathonian of offshore eastern Canada. Two species, *P. laeviscula* and *P. prolongata* [Ex *Strictocythere*], from the Callovian–Oxfordian of India and Madagascar, and the Bajocian of Australia respectively, are known Southern Hemisphere species.

Valid species. We consider the following species (listed in date order) to be valid members of *Progonocythere*. In this, and all subsequent lists of valid species, an asterisk indicates a new combination:

P. stilla Sylvester-Bradley, 1948; Bathonian, Britain (Pl. 1, figs 1–3)

**P. polonica* Blaszyk, 1959; Bathonian Poland (Ex *Strictocythere* (Text-fig. 11–1)

P. ogrodzieniecensis Blaszyk, 1959; Bathonian, Poland

P. laeviscula Ljubimova, Guha and Mohan, 1960; Callovian–Oxfordian, India

P. cristata Bate, 1963; Bajocian, Britain

P. reticulata Bate, 1963; Bajocian, Britain

P. multipunctata Whatley, 1964; Oxfordian, Britain

P. parastilla Whatley, 1964; Oxfordian, Britain

P. acuminata Bate, 1965; Bajocian, Britain

**P. bicarinata* (Bate, 1965); Upper Bajocian, England (Ex *Malzia*) (Pl. 1, figs 8–9)

P. polita Bate, 1965; Bajocian, Britain

**P. unicarinata* (Bate, 1965); Upper Bajocian, England (Ex *Malzia*)

- P. yonsnabensis* Bate, 1965; Bajocian, Britain
P.? *convexa* Blaszyk, 1967; Bathonian, Poland
P. praepolonica Dreyer, 1967; Bajocian, Germany
P. callovica Wienholz, 1967; Callovian, Germany
P. laevigata Bate, 1967; Bathonian, Britain
P. rugosa Bate, 1967; Bathonian, Britain
P. triquetra Bate, 1967; Bathonian, Britain
P. lacazensis Rohr, 1976; Bathonian, France
P. laeviscula Ljubimova, Guha and Mohan, 1960 *sensu* Kulshreshtha *et al.* 1985; Callovian–Oxfordian, India
P. postangusta (Sheppard) *sensu* Dèpêche, 1985; Middle Bathonian, France
P. honigsteini Rosenfeld and Gerry *in* Rosenfeld *et al.* 1987; Bathonian, Egypt
P. aff. parastilla Whatley, 1964 *in* Rosenfeld *et al.* 1987; Oxfordian, Egypt
Progonocythere sp. Dèpêche *et al.*, 1987; Bajocian–Bathonian, Saudi Arabia
P. polonica recta Brand, 1990; Upper Bathonian, Germany
Progonocythere sp. Rosenfeld and Honigstein, 1991; Callovian, Israel
**P. prolongata* (Chapman, 1904) *in* Malz and Oertli 1994; Lower Bajocian, Australia (Ex *Loxoconcha elongata* Chapman, 1904; Ex *Strictocythere*)

Glyptocythere Brand and Malz, 1962

This genus was described by Brand and Malz (1962) based on six species (type species *Glyptocythere tuberodentina*) with entomodont hinge and egg-shaped to trapezoidal valves in lateral view, strongly inflated lateral surface and an ornament with or without strong reticulation, and vertical ribs or only

EXPLANATION OF PLATE 1

- Figs 1–3. *Progonocythere stilla* Sylvester-Bradley; Bathonian, Langton Herring, Dorset, England; The Natural History Museum, Department of Palaeontology. 1–2, 41908, holotype; right valve. 1, external view. 2, internal view. 3, paratype, 41909, external view. All $\times 64$.
 Figs 4–6. *Glyptocythere tuberodentina* Brand and Malz; Bajocian, Germany; Senckenberg Museum, Department of Palaeontology, Frankfurt-am-Main. 4, SMF Xe 4299, holotype; female, left valve, external view. 5, SMF Xe 4306, paratype; female, right valve, internal view. 6, SMF Xe 4306; female, right valve, external view. All $\times 50$.
 Fig. 7. *Majungaella perforata* Grekoff; Portlandian, Madagascar; Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris; H275, holotype; female, right valve, external view; $\times 54$.
 Figs 8–9. *Progonocythere bicarinata* (Bate) (Ex *Malzia*); Upper Bajocian, Yorkshire, England; The Natural History Museum, Department of Palaeontology; Io 1797; female, left valve. 8, external view. 9, dorsal view. Both $\times 59$.
 Figs 10–14. *Fastigatocythere juglandica* (Jones) (Ex *Progonocythere* Whatley; Ex *Cythere* Jones), Upper Bathonian, Oxfordshire. Aberystwyth Micropalaeontological Museum. 10, RCW/Bath/107; female, left valve, external view. 11, RCW/Bath/105; female, right valve, external view. 12, RCW/Bath/109; male, right valve, external view. 13, RCW/Bath/107; female, left valve, internal view. 14, RCW/Bath/102; male, left valve, external view. All $\times 57$.
 Figs 15–16. *Majungaella santacruziana* (Rossi de García, 1972) (Ex *Novocythere*); Aptian–Albian, southern Argentina; topotype from collections of Dirección Nacional Servicio Geológico, Buenos Aires, and now in micropalaeontological collections of Division de Paleozoología Invertebrados, Museo de La Plata, La Plata, Argentina. From type level, borehole Sc-1, at 903–918m, Santa Cruz, Argentina; MLP 0271; female, left valve. 15, external view. 16, internal view. Both $\times 47$.
 Fig. 17. *Fastigatocythere ihopyensis* (Grekoff, 1963) (Ex *Amicytheridea* Bate; Ex *Procytheridea* Grekoff); Middle Callovian, Tanzania. The Natural History Museum, Department of Palaeontology; Io 6251; female, left valve, external view; $\times 70$.
 Figs 18–20. *Fastigatocythere triangulata* (Bate, 1975) (Ex *Amicytheridea*); Callovian, Tanzania; The Natural History Museum, Department of Palaeontology. 18, Io 6116; male, right valve, external view, $\times 64$. 19, Io 6115; male, right valve, internal view; $\times 85$. 20, Io 6114; female, left valve, external view; $\times 69$.



low swellings. In 1966, they reviewed the genus and added 16 new species. It was considered to be typical of the Bajocian and Bathonian, with a geographical distribution extending from Britain, south-eastwards to the Ukraine (Permjakova 1970) and Uzbekistan (Masumov 1973, see *Macrodentina aspera*, pl. 9, fig. 2)

We consider that the following taxa are best removed from the genus and accommodated elsewhere:

1. *Glyptocythere polita* Bate, 1965 (pl. 5, figs 8–11; pl. 6, figs 1–9), from the Bajocian of Britain, closely resembles *Progonocythere* in shape and in its smooth shell surface, with shallow median sulcus, and its convex ventrolateral extension of the carapace like a thin keel. We have included this species in *Progonocythere* although we are well aware that end members of the two genera are morphologically very similar and that convergence between the two is likely.

2. *Glyptocythere juglandica* (Jones) Bate, 1967 (pl. 4, fig. 9), from the Bathonian of Britain, is now *Fastigatocythere* Wienholz.

3. *Glyptocythere? malzi* Dèpêche, 1973 (pl. 2, figs 9–13), from the Bathonian of France, was later considered by her to be *Kinkelina* Martin, 1960 (see Dèpêche 1985, pl. 30, fig. 15); we agree.

4. *Glyptocythere lunensis* Basha, 1980 (pl. 2, figs 5–9), from the Bathonian of Jordan, is *Fastigatocythere* Wienholz.

5. *Glyptocythere? sp.* Malz *et al.*, 1985 (pl. 6, figs 6–8), from the Bathonian of north-west Sardinia, and only figured, more closely resembles *Progonocythere*.

6. *Glyptocythere oblonga* (Basha) *sensu* Rosenfeld and Gerry in Rosenfeld *et al.* 1987 (pl. 4, figs 7–8), from the Bajocian–Bathonian of Israel, should be included in *Fastigatocythere* Wienholz.

Diagnosis of Glyptocythere Brand and Malz, 1962. At present, we do not regard it as necessary to amend the original diagnosis of the genus except to ensure that it includes rather elongate species such as *G. guembeliana* (Jones) in which the ornament is very feeble or almost smooth. A translated synopsis of the original diagnosis is given below.

Carapace medium to large, egg-shaped to trapezoidal in lateral view; subrectangular to elliptical in dorsal view with end marginal borders clearly distinct from strongly inflated lateral surface. Left valve larger than right valve. Dorsal margin medianly vaulted in left valve, overhung by dorso-lateral surface. Ocular features absent. Ornament with or without strong reticulation with separate longitudinal and vertical ribs or low swellings. Avestibulate. Marginal area wide. Usually nine but up to 12 radial pore canals anteriorly, straight, widely spaced and unbranched; three to five posteriorly. Normal pore canals tend to open through elevations in ornament. Hinge entomodont.

Valid species. We consider the following species to be valid members of *Glyptocythere*:

G. auricula Brand and Malz, 1962; Bathonian, Germany

G. dorsicostata Brand and Malz, 1962; Bajocian, Germany

G. rudimenta Brand and Malz, 1962; Bajocian, Germany

G. tenuisulcata Brand and Malz, 1962; Bajocian, Germany

G. tuberodentina Brand and Malz, 1962; Bajocian, Germany (Pl. 1, figs 4–6)

G. tuberosa Brand and Malz, 1962; Bathonian, Germany

G. costata Bate, 1965; Bajocian, Britain

G. scitula Bate, 1965; Bajocian–Bathonian, Britain

G. comes Brand and Malz, 1966; Bathonian, Germany

G. concentrica Brand and Malz, 1966; Bajocian, Germany

G. hieroglyphica Brand and Malz, 1966; Bajocian, Germany

G. interrete Brand and Malz, 1966; Bajocian, Germany

G. meandrica Brand and Malz, 1966; Bajocian, Germany

G. perpolita Brand and Malz, 1966; Bajocian, Germany

G. plicata Brand and Malz, 1966; Bajocian, Germany

G. praecursor Brand and Malz, 1966; Bajocian, Germany

G. regulariformis Brand and Malz, 1966; Bajocian, Germany

G. rugosa Brand and Malz, 1966; Bajocian, Germany

G. similis Brand and Malz, 1966; Bajocian–Bathonian, Germany
G. sowerbyi Brand and Malz, 1966; Bajocian, Germany.
G. trinodis Brand and Malz, 1966; Bajocian, Germany
G. tuscilla Brand and Malz, 1966; Bajocian, Germany
G. umbonata Brand and Malz, 1966; Bajocian, Germany
G. obtusa Lutze, 1966; Bathonian, Germany
G. perpolita magna Blaszyk, 1967; Bajocian–Bathonian, Germany
G. tuberosa angularis Blaszyk, 1967; Bajocian–Bathonian, Germany
G. guembeliana (Jones) in Bate 1967; Bathonian, Britain
G. oscillum (Jones and Sherborn), in Bate, 1969; Bathonian, Britain
G. persica (Jones and Sherborn), in Bate, 1969; Bathonian, Britain
G. aspera (Khaborava) in Permjakova, 1970; Middle Jurassic, Dnieper Don Depression, Russia
G. crassicostata Permjakova, 1970; Middle Jurassic, Dnieper Don Depression, Russia
G. losoviensis Permjakova, 1970; Middle Jurassic, Dnieper Don Depression, Russia
G. multa Permjakova, 1970; Middle Jurassic, Dnieper Don Depression, Russia
G. medisculata Blaszyk, 1972; Bajocian, Poland
G. posterocostata Blaszyk, 1972; Bajocian, Poland
Glyptocythere sp. Blaszyk, 1972; Bajocian, Poland
G. penni Bate and Mayes, 1977; Bathonian, Britain
Glyptocythere sp. Bate, 1978; Bajocian, Britain
G. raasayensis Stevens, 1985; Bajocian, Isle of Raasay, Scotland
G. cf. dorsicostata Brand and Malz *sensu* Dèpêche, 1985; Bathonian, France

Majungaella Grekoff, 1963

The genus *Majungaella* was described by Grekoff (1963) from the Upper Jurassic and Lower Cretaceous of the Majunga Basin, Madagascar with his new Kimmeridgian–Portlandian species, *M. perforata*, as type. He described a second new Madagascan species, *M. nematis*, ranging from the Portlandian to Valanginian. Subsequently, species of *Majungaella* have been described from the Callovian–Portlandian and Albian of Tanzania (Bate and Bayliss 1969); South Africa (Brenner and Oertli 1976; Valicenti and Stephens 1984); the Upper Cretaceous of Australia (Bate 1972); the Lower and Upper Cretaceous of Argentina (Rossi de García and Prosperpio 1980; Kielbowicz *et al.* 1983), and the Albian of the Falkland Plateau (Dingle 1984). *Majungaella* aff. *nematis* Grekoff is cited (not figured) from probable Valanginian strata in southern Chile (Sigal *et al.* 1970). According to its geographical distribution, *Majungaella* is considered to be a genus typical of the Southern Hemisphere.

In the present review, we have encountered several species which we consider would be best removed from the genus and accommodated elsewhere:

1. *M. queenslandensis* Krömmelbein, 1975 (pl. 2, figs 4–6), *M. margaritata* Krömmelbein, 1975 (pl. 1, figs 1–2) and *Majungaella* sp. A Krömmelbein, 1975 (pl. 1, fig. 3), from the Albian–Cenomanian of Australia, were recently described as the new genus *Exposterocythere* Whatley, Ballent and Maybury, 1995b.
2. *Majungaella*? sp. B Krömmelbein, 1975, from the Albian–Cenomanian of Australia, seems to be a juvenile specimen of *Exposterocythere queenslandensis* (Krömmelbein).
3. *Majungaella verseyi* Neale, 1975 (pl. 8, fig. 5; pl. 14, fig. 3; text-fig. 2b), from the Santonian of Australia, is placed in *Exposterocythere* Whatley, Ballent and Maybury, 1995b.
4. *Majungaella brentonensis* (Dingle) *sensu* Guha 1976 (pl. 3, fig. 16a–b), from the Upper Jurassic of Kutch, India, belongs to *Fastigatocythere* Wienholz.
5. *Majungaella*? *minuta* Swain, 1976 (pl. 1, figs 19–21, 23), from the Aptian/Albian of DSDP, north-west Atlantic, has a hemimerodont hinge and is very much smaller ($L = 0.36$ mm) than all other species. This is possibly a *Procytheridea* Peterson.
6. *M. cf. queenslandensis* Krömmelbein in Dingle 1984 (figs 170–187) is conspecific with *Majungaella* sp. A Dingle, 1972 (fig. 4), from the Aptian/Albian of South Africa, and both are included in *Exposterocythere*.
7. *Majungaella*? sp. 327/16 Dingle, 1984 (fig. 18A–C), from the Middle Albian of South Africa, which seems to have an antimerodont hinge, should be referred to the Cytherideidae.

Doubtful species of Majungaella. *Majungaella? hemigymnae* Brenner and Oertli in Dingle 1984 (fig. 17F), from the Aptian of South Africa, is only a fragmentary carapace, and it is not possible, therefore, to assign it to any genus with certainty.

Synonymized genera. In the original description by Grekoff (1963), *Majungaella* is diagnosed as having a robust carapace with surface coarsely punctate and an anterior marginal zone with 14–20 marginal pore canals. Dingle in Dingle and Klingler (1972) and Bate (1975) considered that these canals increase in number from 14–20 in the Jurassic, to 28–30 in the Cretaceous. Krömmelbein (1975) removed from *Majungaella* those Upper Cretaceous species having an increased number of anterior marginal pore canals (24–28) and a distinctive upturned postero-dorsal margin, and placed them in his new genus *Tickalaracythere*. Rossi de García (1972) described *Novocythere* from the Aptian–Albian of southern Argentina, with nearly 25 anterior marginal pore canals but all other characters of her genus appear to be the same as *Majungaella*. We consider that an increase in number of anterior marginal pore canals is not a character sufficient to separate genera; on the contrary, it is a signal of evolution within a genus (cf. within the schulerideinid lineage *Eoschuleridea*–*Schuleridea*–*Aequacytheridea*). We have, therefore, amended the diagnosis of *Majungaella* to accommodate the species of both *Tickalaracythere* and *Novocythere*.

Emended diagnosis of Majungaella Grekoff, 1963. Progonocytherinae with robust carapace; pyriform, subtriangular to trapezoidal in lateral view and postero-dorsally upturned; strongly convex in dorsal view. Lateral surface ornamented by coarse punctae in concentric pattern; ventral surface with longitudinal ribs. Marginal denticles common especially anteriorly. Left valve larger than right. Eye tubercle and shallow post-ocular sulcus present. Hinge entomodont. Anterior marginal pore canals 14–28 or more in number. A very narrow anterior vestibulum may be present.

Stratigraphical range. Callovian to Maastrichtian.

Valid species. We consider the following species to be valid members of *Majungaella*:

**M. mundula* (Grekoff, 1963); Middle Callovian, Madagascar (Ex *Progonocythere*)

M. nematis Grekoff, 1963; Valanginian, Madagascar

M. perforata Grekoff, 1963; Portlandian, Madagascar (Pl. 1, fig. 7)

M. pyriformis Bate and Bayliss, 1969; Albian, Tanzania

M. annula Bate, 1972; Santonian and Campanian, Australia

**M. santacruziana* (Rossi de García, 1972); Aptian–Albian, southern Argentina (Ex *Novocythere*) (Pl. 1, figs 15–16)

M. kimmeridgiana Bate, 1975; Kimmeridgian, Tanzania

M. oxfordiana Bate, 1975; Upper Oxfordian, Tanzania

M. praeperforata Bate, 1975; Kimmeridgian, Tanzania

M. scheibnerovae (Krömmelbein, 1975); Aptian–Albian, Australia. This species is probably a junior synonym of *M. santacruziana* (Rossi de García)

**M. ticka* (Krömmelbein, 1975); Aptian–Albian, Australia (Ex *Tickalaracythere*) (Text-fig. 1A–D)

M. bifurcata Brenner and Oertli, 1976; Valanginian–Hauterivian, South Africa

M. hemigymnae Brenner and Oertli, 1976; Hauterivian, South Africa

M. perforata Grekoff in Guha, 1976; Upper Jurassic, India

M. nematis Grekoff in Guha, 1976; Upper Jurassic, India

M. australis Rossi de García and Proserpio, 1980; ?Upper Campanian–Lower Maastrichtian, southern Argentina

Majungaella A Kielbowicz *et al.*, 1983; Valanginian, Southern Argentina (which we consider to be conspecific with *M. praehemigymnae* Valicenti and Stephens)

M. praehemigymnae Valicenti and Stephens, 1984; Valanginian, South Africa

M. uitenhagensis (Dingle) in Valicenti and Stephens, 1984; Valanginian–Hauterivian, South Africa

M. cf. perforata Grekoff in Rosenfeld and Raab, 1984; Neocomian, Israel

M. mundula (Grekoff) in Kulshreshtha *et al.*, 1985; Callovian–Oxfordian, India

M. biswasi Neale and Singh, 1986; Oxfordian, India

Malzia Bate, 1965

The genus *Malzia* was described by Bate (1965, p. 110), from the Upper Bajocian of England, as *Progonocytherinae* with subquadrate carapace, tapering to posterior margin and with anterior and posterior compressed margins. The ventro-lateral border extended into keel-like projections and there was a low eye swelling. The hinge was entomodont, 2nd anterior marginal pore canals numbered approximately eight.

This genus was erected with two species: the type species, *M. bicarinata* Bate (1965, p. 111, pl. 9, figs 5–8; pl. 10, figs 1–3; text-figs 11–14) having two ventro-lateral keels, and *M. unicarinata* Bate (1965, p. 113, pl. 10, figs 4–10; pl. 11, figs 1–4; text-fig. 15) with only one. Although *Malzia* with its keels somewhat resembles *Marssatourella* Malz, the resemblance is entirely superficial since the latter genus belongs to the Exophthalmocytheridae and differs in hingement and other important internal details.

Comparison of the illustrations of *Malzia* with those of *Progonocythere yonsnabensis* Bate, 1965 (p. 116, pl. 12, figs 5–14; pl. 13, figs 1–4; text-figs 16–19) and *Progonocythere acuminata* Bate, 1965 (p. 114, pl. 2, figs 5–10; pl. 12, figs 1–4), both from the Bajocian of England, shows that *Malzia* is merely *Progonocythere* with ventro-lateral keel-like projections. The amended diagnosis of *Progonocythere* (see above) includes *Malzia*.

Fastigatocythere Wienholz, 1967

This genus was based mainly on species with inverted chevron-type ornament, pronounced post-ocular sulcus and entomodont hinge. In addition to the type species, *F. rugosa* from the Callovian of north-west Germany, and *Progonocythere juglandica juglandica* (Jones) from the Middle Jurassic of Europe, Wienholz (1967) also included the following Middle Jurassic Madagascan species of Grekoff (1963): *Progonocythere accessa*, *P. bicrucata*, *P. befotakaensis*, *Progonocythere* 2393 and *P. juglandica malgachica*. Since 1967, there have been many more records of the genus. In our opinion, those which follow should be excluded.

1. *Lophocythere interrupta* Triebel, 1951 (pl. 47, figs 35–41) from the Callovian of Europe, has been placed by a number of authors in *Fastigatocythere*. However, we agree with Whatley (1970, p. 335) that it conforms to the diagnosis of *Lophocythere* Sylvester-Bradley and should certainly be retained there.

2. Dèpêche (1973, p. 216) relegated *Fastigatocythere* to the position of a subgenus of *Lophocythere* Sylvester-Bradley but we retain it here as a distinct genus. Both *Lophocythere* (*Fastigatocythere*) *bessinensis* Dèpêche, 1973, pl. 1, figs 3–8 and *Lophocythere* (*Fastigatocythere*) *rimosa* Dèpêche, 1973, pl. 1, figs 9–13), from the Lower Bathonian of France belong, in our opinion, to *Neurocythere* Whatley.

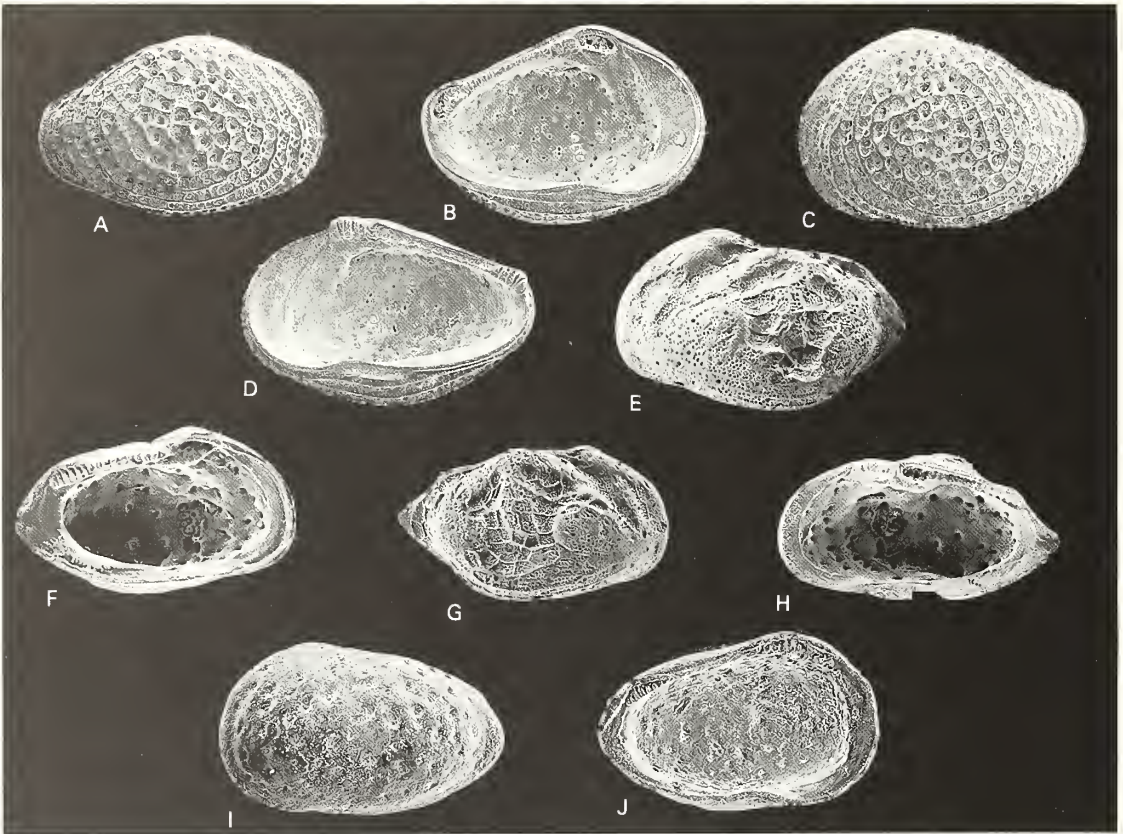
3. *Fastigatocythere? grekoffi* Brenner and Oertli, 1976 (pl. 6, fig. 5–12; pl. 8, fig. 6), from the Valanginian of South Africa, is certainly *Majungaella* Grekoff.

4. *Fastigatocythere interrupta interrupta* (Triebel, pl. 4, figs 5–6) and *F. interrupta* subsp. A (Lutze), pl. 4, figs 8–9, both in Herngreen *et al.* (1983–1984), from the Middle Callovian of the eastern Netherlands should be retained in *Lophocythere* Sylvester-Bradley. (See 1. above).

5. *Fastigatocythere nafaliensis* Rosenfeld and Raab, 1984 and Rosenfeld *et al.* 1988, from the Lower Cretaceous of Israel, seems to have an antimerodont hinge and possibly belongs to *Neocythere* Mertens.

Doubtful species of Fastigatocythere. *Fastigatocythere?* sp. Neale and Singh, 1985 (pl. 2, fig. 11), from the Oxfordian of India, is particularly difficult to place generically due to the inadequacy of its illustration.

Synonymized genera. The diagnosis of *Fastigatocythere* is herein amended to accommodate the species of *Amicytheridea* Bate; *Glyptogatocythere* Basha; and *Zerqacythere* Basha.



TEXT-FIG. 1. A-D, *Majungaella ticka* (Krömmelbein) (Ex *Tickalaracythere*); Australian Geological Survey Organisation, Canberra. A, D, CPC 13868, holotype; male, right valve, external (A) and internal (D) views; $\times 34$ and $\times 39$. B-C, CPC 13869, paratype; female, left valve, internal (B) and external (C) views; $\times 43$. E-H, *Dromocythere sagittata* Ware and Whatley, 1980; Upper Bathonian, Oxfordshire, England; The Natural History Museum, Department of Palaeontology. E-F, OS 11337, holotype; female, left valve, external (E) and internal (F) views; $\times 102$. G, OS 11338, paratype; female, right valve, external view; $\times 91$. H, OS 11343, paratype; female, right valve, internal view; $\times 91$. I-J, *Progonocythere polonica* Blaszyck, 1959 (Ex *Strictocythere*); Bathonian, France; British Geological Survey, Keyworth, Nottingham, England. I, MPK 3683; female, left valve, external view; $\times 59$. J, MPK 3684; female, left valve, internal view; $\times 59$.

Emended diagnosis of Fastigatocythere Wienholz, 1967. *Progonocytherinae* with subtriangular to subrectangular lateral outline; ornamented by ribs in inverted chevron which overreach dorsal margin and may be broken up centrally into coarse reticulation creating prominent tubercles. Ventrally punctate or with ribs parallel to ventral margin. Eye tubercle and marked post-ocular sulcus. Left valve larger than right. Anterior marginal pore canals normally seven to nine, but range up to 14. Avestibulate. Frontal scar anterodorsal in position, usually circular.

Distribution. *Fastigatocythere* Wienholz is a typical Middle and Upper Jurassic genus with a wide stratigraphical and geographical distribution. In the Northern Hemisphere, it has been recognized mainly from the Bathonian–Kimmeridgian of Britain, continental Europe, Egypt, Jordan and Saudi Arabia; it is also recorded (not illustrated) from the Callovian and Oxfordian of offshore eastern Canada (Ascoli 1988, p. 26). In the Southern Hemisphere, it is recognized from the Bathonian–Kimmeridgian of East and South Africa, Madagascar and India, and also from the Lower Bajocian of Australia. From the Middle Callovian of Argentina, there is one species

(*Progonocythere neuquenensis* Musacchio) which, at present, we assign tentatively to *Fastigatocythere* Weinholz.

Valid species. We consider the following species to be valid members of *Fastigatocythere*:

F. rugosa Wienholz, 1967; Lower Callovian, Germany

**F. accessa* (Grekoff, 1963); Bathonian–Callovian, Madagascar (Ex *Progonocythere*)

**F. bicrucata* (Grekoff, 1963); Bathonian–Callovian, Madagascar (Ex *Progonocythere*)

**F. befotakaensis* (Grekoff, 1963); Bathonian–Callovian, Madagascar (Ex *Progonocythere*)

**Fastigatocythere* 2393 (Grekoff, 1963); Bathonian–Callovian, Madagascar (Ex *Progonocythere*)

F. juglandica juglandica (Jones) in Wienholz, 1967; Middle Jurassic, Europe and Madagascar (Pl. 1, figs 10–14)

F. juglandica malgachica (Grekoff, 1963); Bathonian–Callovian, Madagascar

F. aff. bretonensis (Dingle) in Bate, 1975; Middle–Upper Kimmeridgian, Tanzania

**F. ihopyensis* (Grekoff) in Bate 1975, Bathonian–Callovian, East Africa, India and Madagascar (Ex *Amicytheridea*) (pl. 1, fig. 17)

**F. triangulata* (Bate, 1975); Callovian, East Africa and Madagascar (Ex *Amicytheridea*)

Fastigatocythere sp. Guha; 1976, ?Bathonian, India

F. accessa (Grekoff); in Guha, 1976, Upper Jurassic, India

Lophocythere (*Fastigatocythere*) *aff. juglandica* (Jones) in Rohr, 1976; Bathonian, southern France

**F. malzi* (Basha, 1980); Bathonian, Jordan and Egypt (Ex *Glyptogatocythere*)

F. naftaliensis Rosenfeld and Raab, 1984; Neocomian, Israel

Fastigatocythere sp. Dèpêche, 1985; Middle Bathonian, France

F. bakeri (Basha) in Rosenfeld *et al.*, 1987; Bathonian, Egypt

**F. oblonga* (Dèpêche, Le Hindre, Manivit and Vaslet, 1987); Middle Callovian, Saudi Arabia (Ex *Amicytheridea*)

**F. dierallaensis* (Basha, 1980) form A Dèpêche *et al.*, 1987; Bajocian, Saudi Arabia (Ex *Amicytheridea*)

**F. dierallaensis* (Basha, 1980) form B Dèpêche *et al.*, 1987; Upper Callovian, Saudi Arabia (Ex *Amicytheridea*)

**F. dhrumaensis* (Dèpêche, Le Hindre, Manivit and Vaslet, 1987); Bajocian, Saudi Arabia (= *Glyptogatocythere magharaensis* Rosenfeld and Gerry in Rosenfeld *et al.*, 1987) (Ex *Amicytheridea*)

**F. triangula* (*sic*) (Bate) in Dèpêche *et al.*, 1987; Upper Callovian, Saudi Arabia (Ex *Amicytheridea*)

F. juglandica (Jones) Brand 1990; Upper Bathonian, north-west Germany

F. grossepunctata (Chapman) in Malz and Oertli, 1994; Lower Bajocian, Australia

F. subiehensis (Basha, 1980); Bathonian, Jordan, Egypt and Saudi Arabia (Ex *Zerqacythere*)

F. huniensis (Basha, 1980, pl. 4, figs 12–14); Bathonian, Jordan (Ex *Zerqacythere*); herein given the new name *Fastigatocythere jordanica*. This is necessary because Basha gave both a *Glyptocythere* species and a *Zerqacythere* species the name *huniensis*. Since we have decided that both belong to *Fastigatocythere*, one must be given a new name.

F. magharaensis (Rosenfeld and Gerry in Rosenfeld *et al.*, 1987); Bajocian, Egypt

Fastigatocythere sp. Khosla and Jakhar, 1994 (fig. 4, 6–8); Upper Bathonian–Callovian, Kutch, India

Novocythere Rossi de García, 1972

The genus *Novocythere* was described by Rossi de García (1972, p. 271, pl. 1, fig. 7), from the Aptian–Albian of well SC-1, southern Argentina, with *N. santacruciana* as type species. According to the original description, the genus is pyriform, postero-dorsally upturned, strongly convex in dorsal view and ornamented by concentric puncta. Marginal denticles are present and the hinge is entomodont. The vestibulum is small and there are nearly 25 marginal pore canals anteriorly.

The same author (1977, p. 117, pl. 1) re-illustrated the genus using SEM and pointed out some further aspects of the morphology and age of *Novocythere*. At the same time, she differentiated it from *Majungaella* Grekoff and *Tickalaracythere* Krömmelbein on the basis of its lack of an eye tubercle and presence of an anterior vestibulum. However, her illustrations show that the type material has a low elongate ocular swelling which we interpret as an eye tubercle. With reference to the vestibula, no mention is made of this feature in the type description of *Majungaella* and, ironically, *Majungaella australis* Rossi de García and Proserpio, 1980 clearly shows a narrow anterior vestibulum. In the absence of any morphological criteria to separate this monospecific genus from *Majungaella*, we subsume it herein as a junior synonym.

Amicytheridea Bate, 1975

This genus, from the Middle Callovian of Tanzania, East Africa, was erected by Bate (1975) with *Procytheridea ihopyensis* Grekoff, 1963 as type species. *A. triangulata* Bate = *Procytheridea*? 3330 Grekoff, 1963, also from the Middle Callovian of East Africa, was also designated.

As diagnosed by Bate (1975, p. 91), *Amicytheridea* has a robust carapace, triangular in lateral outline and convex in dorsal view, with dorso-lateral ribs in an inverted chevron. The left valve is larger than the right. The eye tubercle and oblique post-ocular sulcus are clearly marked. The hinge is lobodont (with antero-median element loculate in the right valve). The anterior marginal pore canals number approximately 14.

Although he claimed that the hinge of *Amicytheridea* is lobodont, it can be seen (Bate 1975, p. 193, fig. 11a–c) to be also entomodont. In fact, the difference between the two hinge types is only a matter of degree; in the lophodont hinge, the denticles on the antero-median element of the left valve are more distally expanded than in an entomodont hinge. We would not regard this as a generic character. In our opinion, *Amicytheridea* is synonymous with *Fastigatocythere* Wienholz, mainly because of its subtriangular shape, dorso-lateral inverted chevron ornament, ventro-lateral ribs parallel to the ventral margin, and clear eye tubercle and post-ocular sulcus. The antennal scar, however, is situated antero-centrally.

The emended diagnosis of *Fastigatocythere* (see above) includes *Amicytheridea* whose species are transferred and listed thereunder.

Tickalaracythere Krömmelbein, 1975

The genus *Tickalaracythere* was defined by Krömmelbein (1975) with two species, *T. ticka* (the type) and *T. scheibnerovae*, both from the Albian–Cenomanian of the Great Artesian Basin, Queensland, Australia. It has also been cited but not illustrated from the Campanian–Maastrichtian of the Sergipe Basin, eastern Brazil (Krömmelbein 1976, p. 546).

Krömmelbein (1975) erected this genus to separate from *Majungaella* some Upper Cretaceous species with robust and trapezoid-pyriform carapaces, which were postero-dorsally upturned, strongly convex in dorsal view, ornamented by a concentric pattern of punctations, with eye tubercle, shallow post-ocular sulcus and marginal denticles. Their hinges are entomodont, anterior pore canals range in number from 24 to 28, and an anterior vestibulum is present in males. We believe these characters, in the context of the total range of characters within the plexus of *Majungaella* and *Tickalaracythere*, to be specific and not generic. Consequently, we regard *Tickalaracythere* as a junior synonym of *Majungaella* and have emended the generic diagnosis of the latter accordingly (see also Whatley *et al.* 1995a). Species previously assigned to *Tickalaracythere* are accordingly transferred, and listed under *Majungaella* (see above).

Glyptogatocythere Basha, 1980

The genus *Glyptogatocythere* was erected by Basha (1980, p. 241) with *G. malzi*, from the Bathonian of Jordan, as type species. Rosenfeld and Gerry in Rosenfeld *et al.* (1987, p. 260) described a second species, *G. magharaensis*, from the Bajocian of Egypt. As diagnosed, *Glyptogatocythere* Basha is subtriangular, ovate, centrally inflated in a triangular form; it is ornamented by subtriangular ribs in an inverted chevron with marked eye tubercle and oblique post-ocular sulcus. The left valve is larger than the right. The hinge is entomodont.

According to the type description and illustrations of *Glyptogatocythere*, we consider it to be synonymous with *Fastigatocythere* Wienholz, and its species are transferred.

Zerqacythere Basha, 1980

Basha (1980, p. 251) first described the genus with *Z. subiehiensis* as type species and with another new species, *Z. huniensis*; both came from the Bathonian of Jordan.

As diagnosed, this genus has a subtriangular carapace with a surface ornamented by sub-triangular ribs, in an inverted chevron, which overreach the dorsal margin and develop into complicated reticulation supported by two to three prominent, raised tubercles; the eye tubercle is prominent and there is a pronounced oblique post-ocular sulcus. The hinge, while allegedly lobobont, is clearly entomodont.

We consider that *Zerqacythere* is merely *Fastigatocythere* in which the ribs are broken up centrally into coarse reticulation creating prominent tubercles. We have, therefore, placed the two species of *Zerqacythere* within *Fastigatocythere* and consider the genus as a junior synonym. The emended diagnosis of *Fastigatocythere* Wienholz (see above) includes *Zerqacythere*, whose species are listed thereunder.

Dromacythere Ware and Whatley, 1980

This genus was separated by Ware and Whatley (1980) from its apparent closest relative, *Fastigatocythere* Weinholz, 1967. Named for its 'humped' dorsal margin, *Dromacythere* differs from *Fastigatocythere* and from other progonocytherids in its small size (0.41–0.48 mm adult length), exceptionally strongly developed entomodont hinge and the very strongly developed eye tubercle. *Arkellicythere* Ware and Whatley, 1980 is also small but has many more radial pore canals (18–22 anteriorly as opposed to eight anteriorly in *Dromacythere*). It was originally thought to be a progonocytherid but re-examination of its hinge has shown it to be antimerodont and the genus is, thereby, excluded from the family. It is possibly a protocytherid.

Dromacythere sagitta Ware and Whatley, 1980 (Text-fig. 1E–H) is the type and only known species of the genus, which does not seem to be particularly close to the other genera in the complex we have considered here. The following generic diagnosis is after Ware and Whatley, 1980. Small, subquadrate to globose, dimorphic, ornamented, progonocytherid, dorsally umbonate, with an eye tubercle and prominent post-ocular sinus. Radial pore canals few, straight, widely spaced. Hinge strongly entomodont, muscle scars type A (Bate 1963). Monotypic.

Strictocythere Sheppard in Brand, 1990

The genus *Strictocythere* was introduced by Sheppard (1981, p. 59) in her unpublished doctoral thesis to accommodate a group of species previously assigned to *Progonocythere*. Brand (1990, p. 207) used this name under the authorship of 'Sheppard in Brand'. Brand differentiated two subspecies from the type species *Progonocythere polonica*, *S. polonica polonica* (Błaszyk) and *S. polonica recta* Brand, both of them from the Upper Bathonian of north-west Germany (Brand 1990, pl. 13, figs 8–15 and figs 16–21 respectively). Malz and Oertli (1994, pl. 1, figs 4–5) described '*Strictocythere prolongata*' (nom. nov. pro *Loxoconcha elongata* Chapman, 1904) from the Lower Bajocian of Australia.

As diagnosed by Sheppard (1981) and emended by Brand (1990), *Strictocythere* is elongate-oval in shape, with anterior and posterior compressed margins, well rounded anterior margin and rounded triangular posterior margin with a short caudal process. The ventro-lateral border of valves slightly overhangs the ventral margin; the ornament is pitted and the hinge is entomodont.

We consider that *Strictocythere* is merely *Progonocythere* with elongate-oval lateral outline. Our emended diagnosis of *Progonocythere* incorporates the species of *Strictocythere* Sheppard in Brand and the genus is, thereby, subsumed.

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EDITORIAL NOTE

Text-figure 1 was originally submitted as a plate and included illustrations of type material of species described by Basha (1980). This material is housed in the Department of Geology, University of Jordan, Amman, but lacks catalogue numbers. It is the policy of this journal not to publish illustrations of uncatalogued material.

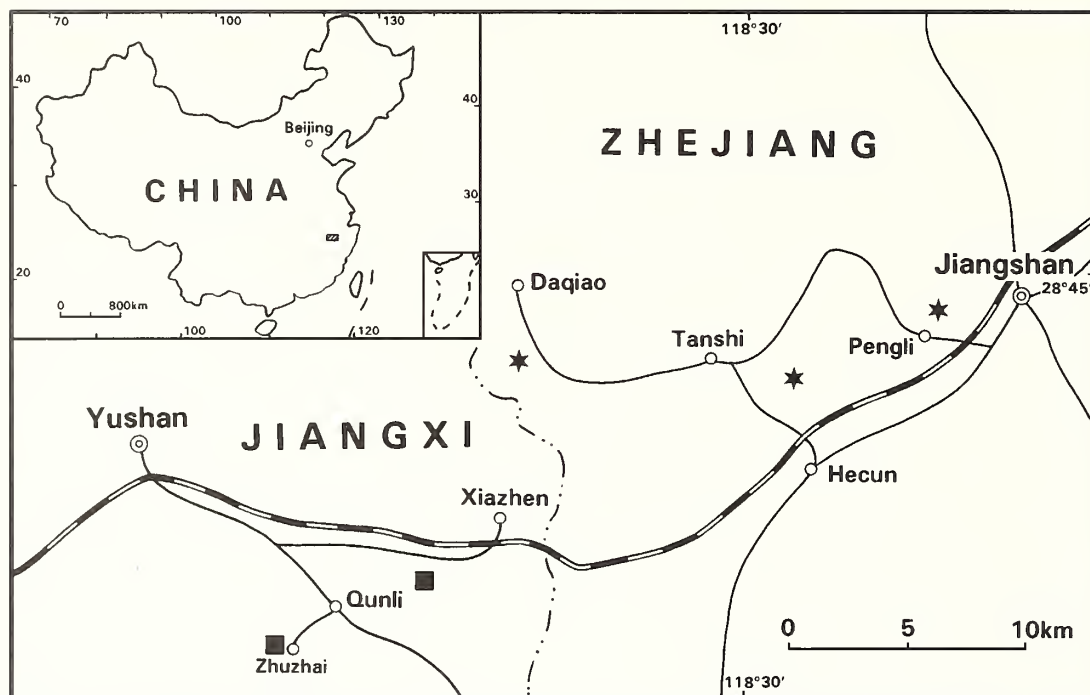
BRACHIDIA OF LATE ORDOVICIAN AND SILURIAN EOSPIRIFERINES (BRACHIOPODA) AND THE ORIGIN OF THE SPIRIFERIDES

by RONG JIA-YU and ZHAN REN-BIN

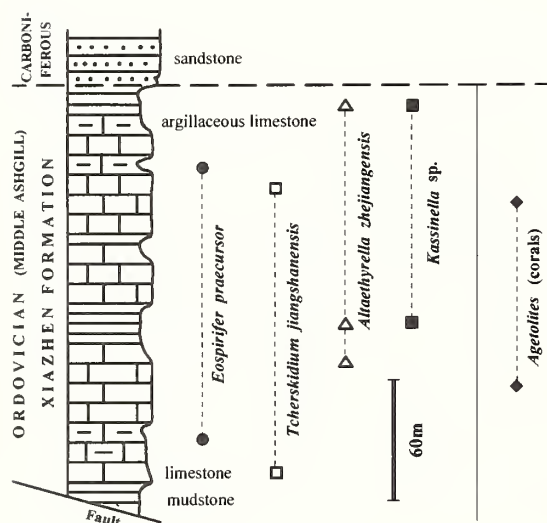
ABSTRACT. The brachidium is revealed for the first time in the Late Ordovician *Eospirifer praecursor*, the earliest known eospiriferine and probably the ancestor of the entire *Spirifer* group. The adult stages of the species possess a spirulum directed ventro-laterally with a pair of small jugal processes without a jugum. The brachidium of the other five species of *Eospirifer* (including *E. radiatus* (Sowerby), the type species) and three of *Striispirifer* (including *S. plicatellus* (Linnaeus)) from the Llandovery, Wenlock or Ludlow in South China, Kazakhstan, England, Sweden and Canada are also revealed and reconstructed, demonstrating the same type of brachidium as in *E. praecursor*. The structure of the early brachidial growth stage of *E. praecursor* is similar to that of the adult stages of the early atrypoid *Cyclospira bisulcata* (Emmons). This, coupled with the evidence of cardinalia, is of significance in the evaluation of eospiriferine origins. A shallow-water environment is proposed for the origination of the Spiriferida. *Eospirifer*, a progenitor and Lazarus genus, probably originated in East and Central Asia in the mid Ashgill; it disappeared in the late Ashgill, but survived the latest Ordovician mass extinction, recovered in Asia and Australia in the Early–Mid Llandovery, and did not spread to Europe and America until the later Llandovery (about the *sedgwickii* Biozone). A striated cardinal process is also seen for the first time in the topotype of *E. radiatus*, indicating that its presence may not be of fundamental significance in the generic classification of the eospiriferine group.

RECENTLY Rong *et al.* (1994) described the oldest known eospiriferine species, *Eospirifer praecursor*, from the Upper Ordovician (middle Ashgill) Changwu Formation, Pengli, Jiangshan, south-western Zhejiang Province, East China (Text-fig. 1). It is the first reliable record of the eospiriferines in the Ordovician and it verifies that the eospiriferines, the earliest representatives of the *Spirifer* group, made their first known appearance in the mid Ashgill, Late Ordovician. It was not possible, however, to make serial sections to reveal the brachidium of *E. praecursor* since the material studied and figured in 1994 is composed only of external and internal moulds of both valves (collected by the present authors during their first field excursions to the area in 1991).

A large quantity (nearly 5000 individuals) of conjoined valves of *E. praecursor* was gathered from three bedding planes of calcareous mudstone in the Xiazhen Formation, Zhuzhai, 15 km south-east of Yushan County Town, north-eastern Jiangxi Province, East China (Text-fig. 1) by Zhan Ren-bin and Fu Li-pu in 1992, and by the present authors in 1994. Within the Xiazhen Formation occur other genera of brachiopods (such as *Tcherskidium*, *Altaethyrella*, *Kassinella*) and corals (*Agetolites*), suggestive of a mid Ashgill age for this formation (Text-fig. 2). Discoveries of conjoined valves have now made serial sectioning possible. More than 30 specimens of this species have been sectioned systematically to reveal the internal morphology of ventral and dorsal valves in a state of good preservation. The purpose of this paper is to show the internal structures of *E. praecursor*, in particular the brachidium. Comparisons of the brachidium of the Late Ordovician *E. praecursor* with Silurian (Llandovery, Wenlock and Ludlow) eospiriferines from South China, Kazakhstan, England, Sweden, and East Canada (Text-fig. 3; Appendix) are also made in this paper. These include some species of *Eospirifer* Schuchert, 1913 and *Striispirifer* Cooper and Muir-Wood, 1951 with *Hedeina* Boucot, 1963 (subjective synonym of *Striispirifer*; see



TEXT-FIG. 1. Location of the study area where *Eospirifer praecursor* was collected. Stars indicate localities yielding specimens preserved as moulds; squares localities with conjoined values.



TEXT-FIG. 2. Stratigraphical distribution of *Eospirifer praecursor* along with other main taxa at the Zhuzhai section, Yushan, north-eastern Jiangxi Province, East China.

Bassett and Cocks 1974). The origin of the eospiriferines is further discussed based on new data from comparisons of the brachidia of the earliest known eospiriferines with some related groups.

The brachidium of the eospiriferines was often neglected by palaeontologists when they studied this group and their external morphology has become the most important basis for their classification. Discoveries of a pair of small jugal processes in *E. praecursor* and *E. radiatus*

TEXT-FIG. 3. Stratigraphical range of species assigned to *Eospirifer* and *Striispirifer* studied in this paper.

SYSTEM	SERIES		<i>Eospirifer</i>	<i>Striispirifer</i>
SILURIAN	PRIDOLI			■ <i>yunnanensis</i>
	LUDLOW			■ <i>plicatellus</i>
	WENLOCK		● <i>radiatus</i> (Gotland) ● (England)	
	LLANDOVERY	Telychian	● cf. <i>radiatus</i>	
		Aeronian	● <i>songkanensis</i>	
		Rhuddanian	● <i>minutus</i>	■ <i>acuminiplicatus</i>
			● <i>sinensis</i>	
ORDOVICIAN	ASHGILL	Late	● <i>cinghizicus</i>	
		Middle	● <i>praecursor</i>	
		Early		

(Sowerby) examined in this paper, support an observation made by Boucot (1963) but are not in accordance with that given by St Joseph (1935) who illustrated a band between two primary lamellae of the spiralia in *E. radiatus* (p. 322, text-fig. 3). Discussions on the real nature of the brachidia in different species of eospiriferines will be given below. The internal morphology of nine taxa of eospiriferines (see Appendix) is revealed in terms of the technique of serial sections using rapid-drying, acetate peels and a camera-lucida microscope (Wild Heerbrugg). A dorsal three-dimensional view of the brachidium of the dorsal valve in eospiriferine species has been reconstructed by tracking various points of different positions of the structures from transverse section planes into longitudinal, commissure planes. The lateral views of the brachidial reconstructions have also been produced by the same method, but normally only the right spiralium, as viewed into the dorsal valve, has been drawn.

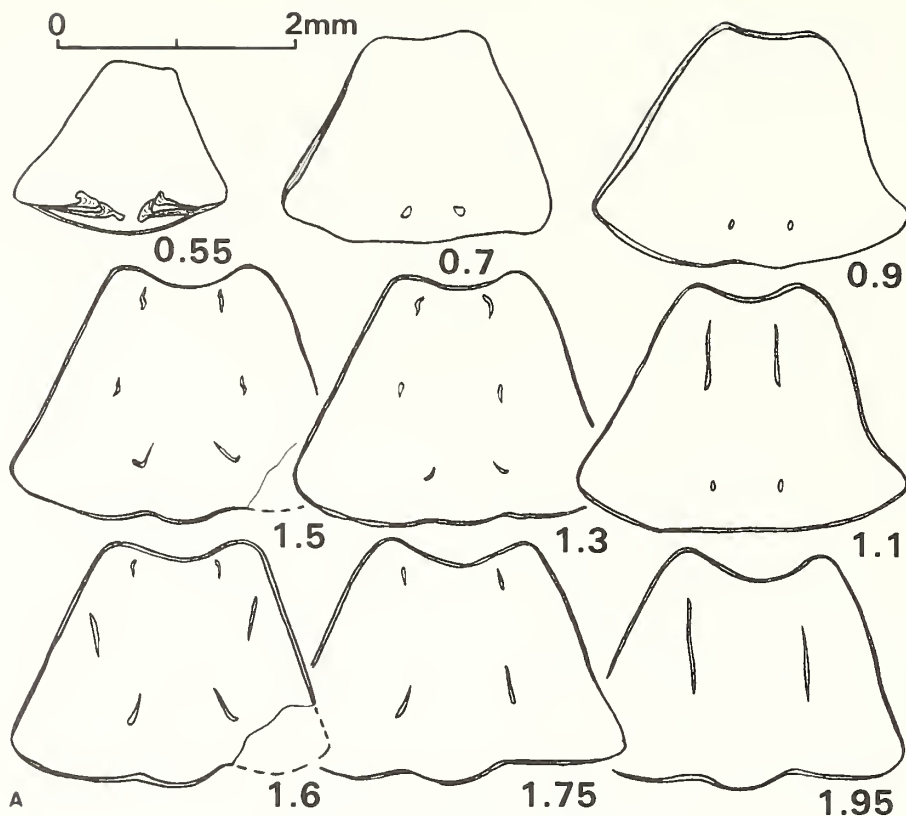
NEW OBSERVATIONS ON *EOSPIRIFER PRAECURSOR*

More than 30 specimens of the Ashgill *E. praecursor* Rong, Zhan and Han, 1994 have been sectioned, and selected serial transverse sections of two specimens of conjoined valves are illustrated in this paper. Text-figure 4A–B illustrates a larger adult shell (6.45 mm wide) and one of the smallest young shells (2.9 mm wide). Brachidia of the two specimens are reconstructed in Text-figure 5A–B. New observations are made on the crura, primary lamellae, spiralia and jugal processes in the following section.

Crura and primary lamellae. The plates supporting crural bases are basically lacking and thus the crura are located freely posteriorly; the crura and primary lamellae are slightly divergent (30–40°), adjacent to the dorsal valve, extending near the anterior commissure, and afterwards turn and curve ventrally and then posteriorly to form spiralia.

In the early stages (Text-figs 4A, 5A), crura are rod-like posteriorly; central inclination is not prominent. Starting from a position close to the junction of the crura and primary lamellae, the crura become plate-like, noticeably concave ventrally, and are moderately inclined internally, with an angle of 80° at the point of transition, where the primary lamellae are less inclined internally (40°, becoming subparallel anteriorly).

In the adult stages (Text-figs 4B, 5B), crura are rod-like posteriorly and then plate-like near the junction of the crura and primary lamellae, slightly concave ventrally at their lateral ends, and strongly inclined centrally, with an angle of about 110°; afterwards the crura are prolonged anterior to the primary lamellae of the spiralia, and the thin, plate-like primary lamellae are posteriorly more



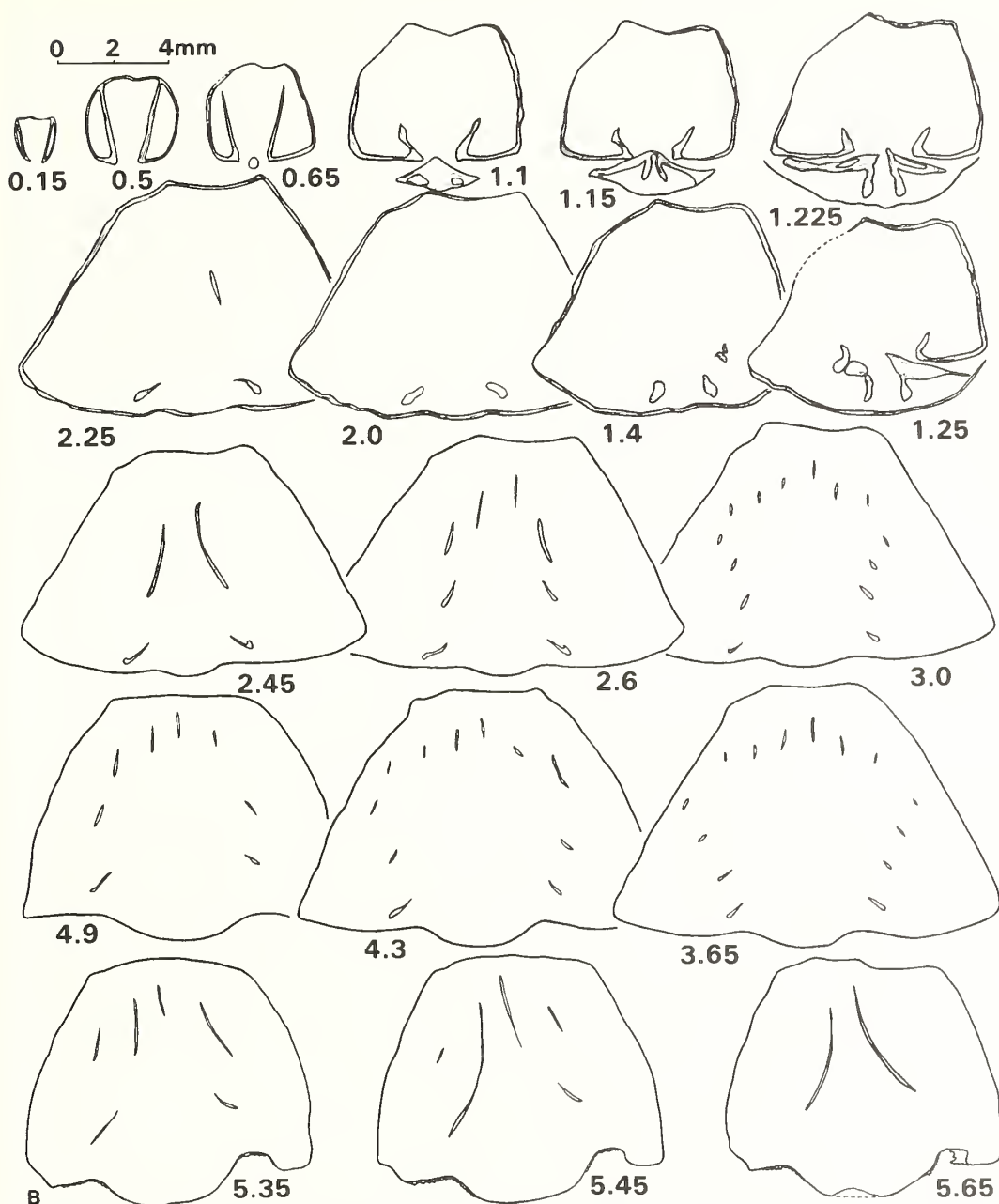
TEXT-FIG. 4A. For caption see facing page.

strongly inclined internally, with an angle of $120\text{--}130^\circ$, and then turn to be less inclined internally, with an angle of $110\text{--}100^\circ$ anteriorly.

Spiralium and jugal process. The most important and significant discoveries are the lophophore supports (brachidium) which have to date not been described in the early eospiriferines (Ashgill to early Mid Llandovery). Our new discoveries demonstrate that the brachidium of *E. praecursor* in adult stages is essentially the same as that of the Silurian eospiriferines examined by Boucot (1963) and the present authors. The brachidium is characterized by the following features: (1) continuous calcite growth from crura to spiralia with the junction between them commonly smooth and not sharply geniculate; (2) a spiralium consisting of only one-and-one-half whorls in very small individuals (Text-fig. 5A) and of three to four whorls in adult specimens (Text-fig. 5B), the axis of the spires being directed laterally in early stages and ventro-laterally in adult stages; the spires lying as a whole nearer the ventral valve; the first whorl almost touching the inner walls of the ventral valve; the spires in the early stages located outside the primary lamellae and in the adult stages located not only outside but within the space between the divergent primary lamellae; (3) a pair of very small, separated jugal processes acuminate centro-ventrally in the adult, but not seen in very small individuals (less than 3.0 mm wide); (4) the lack of any kind of jugum.

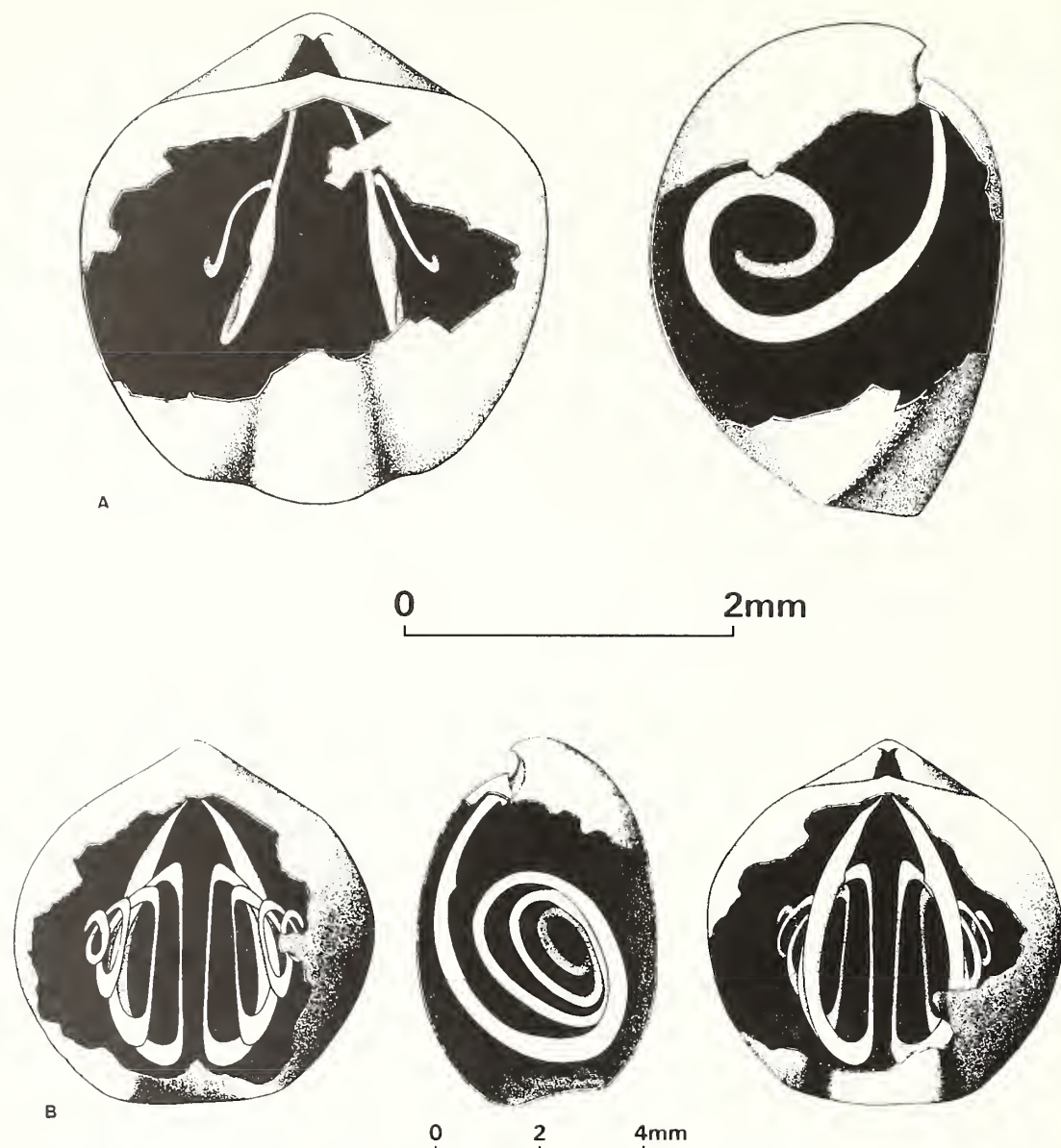
BRACHIDIUM OF OTHER EARLY EOSPIRIFERINES

Serial transverse sections of topotype specimens of some species of *Eospirifer* have been made (see Appendix), including: (1) *Eospirifer cinghizicus* Borisiak (Early Llandovery); (2) *E. sinensis* Rong,



TEXT-FIG. 4A–B, serial transverse sections of two specimens of *Eospirifer praecursor* Rong, Zhan and Han, 1994. Xiazhen Formation (middle Ashgill), Zhuzhai, Yushan. A, for the smaller specimen (length 3.1 mm, width 2.9 mm, depth 2.2 mm), NIGP 124766 (10 sections made and 9 selected herein). B, for the larger specimen (length 6.5 mm, width 6.45 mm, depth 4.45 mm), NIGP 124767 (57 sections made and 19 selected herein).

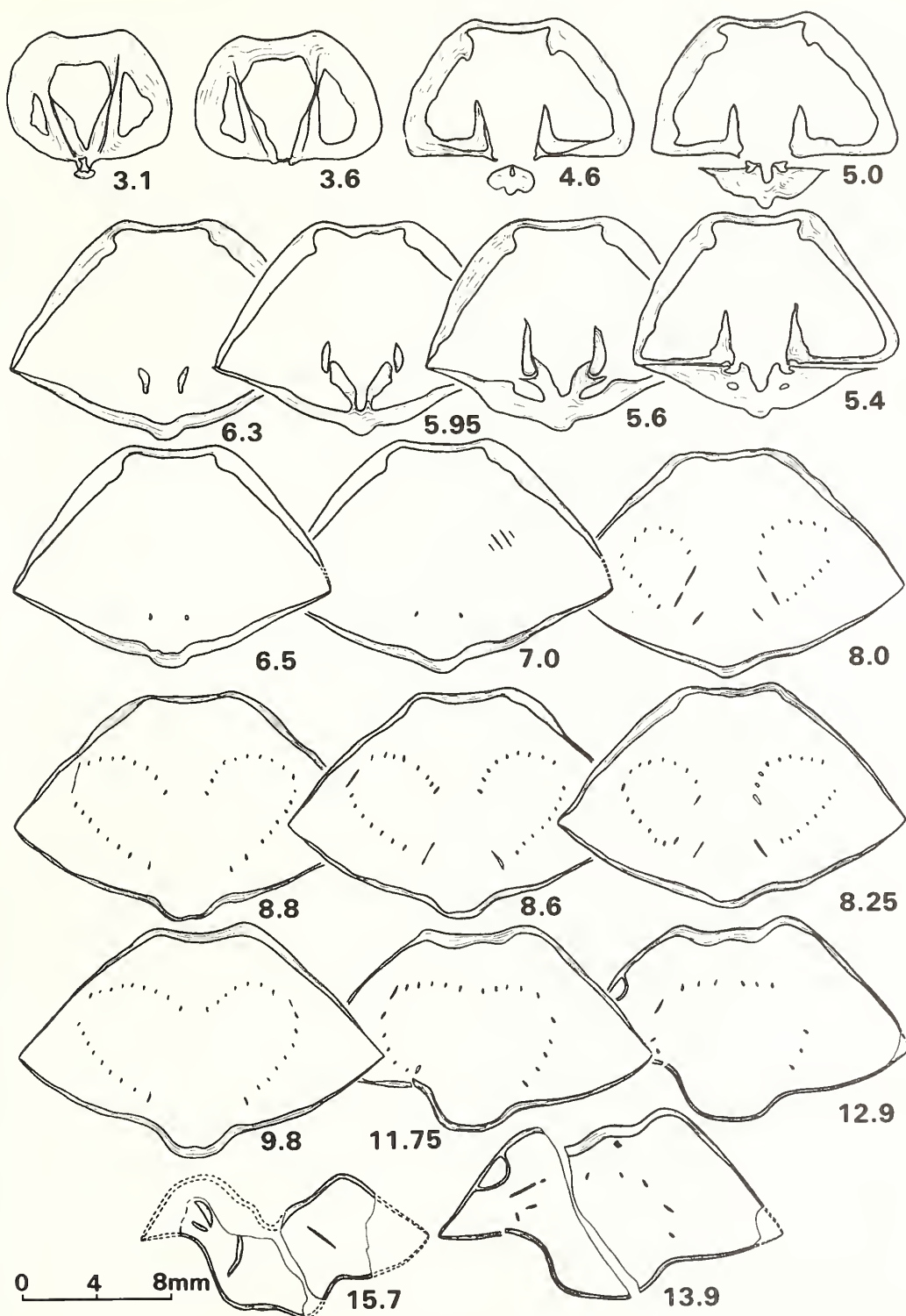
Xu and Yang (late Rhuddanian, Early Llandovery); (3) *E. minutus* Rong and Yang (early Aeronian, Mid Llandovery); (4) *E. songkanensis* Wu (late Aeronian, Mid Llandovery); (5) *E. cf. radiatus* (Sowerby) (Late Llandovery) and (6) *E. radiatus* (Sowerby) (Late Wenlock; both British and



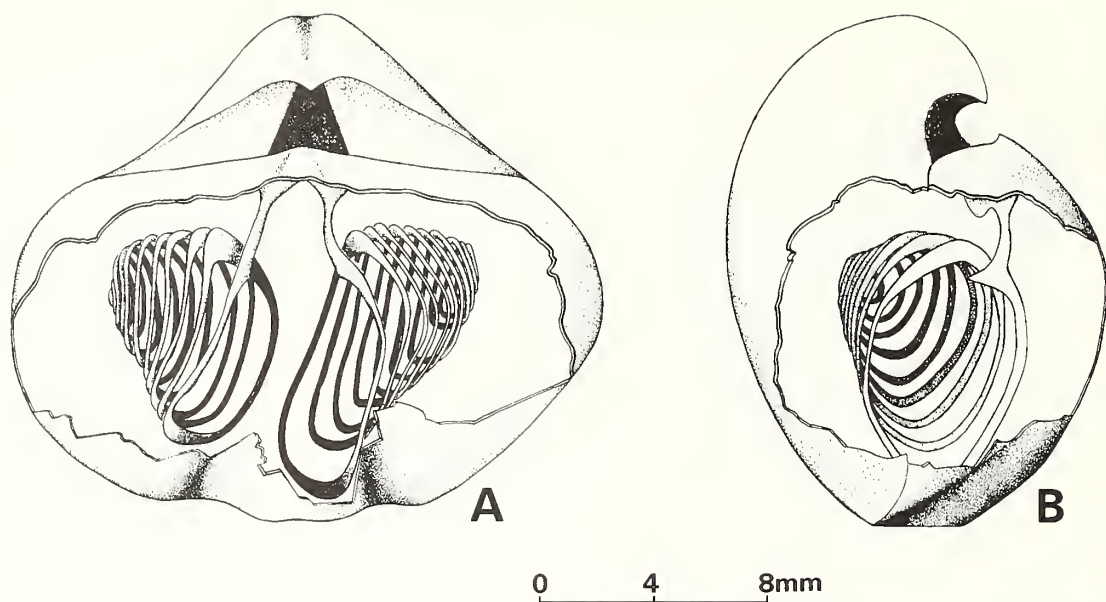
TEXT-FIG. 5A-B, reconstruction of brachidia of two specimens of *Eospirifer praecursor* Rong, Zhan and Han, 1994 based on Text-figure 4A-B respectively. Note the simple spiralium in the smaller specimen (A; lateral view shows only one-and-one-half whorls).

Swedish specimens). Reconstructions of all their brachidia, except for those of *E. cinghizicus* and *E. songkanensis*, are made based on these sections. New investigations reveal that the brachidium of the Llandovery and Wenlock taxa of *Eospirifer* is of the same type as that of Late Ordovician *E. praecursor*.

TEXT-FIG. 6. Serial transverse sections of one specimen of *Eospirifer sinensis* Rong, Xu and Yang, 1974 (length 16.6 mm, width 19.9 mm, depth 11.7 mm); NIGP 124768 (65 sections made and 19 selected herein); Lower Xiangshuyuan Formation (upper Rhuddanian), Leijiatun, Shiqian, north-eastern Guizhou, South-west China.



TEXT-FIG. 6. For caption see opposite.



TEXT-FIG. 7. Reconstruction of brachidia of one specimen of *Eospirifer sinensis* Rong, Xu and Yang, 1974 based on Text-figure 6.

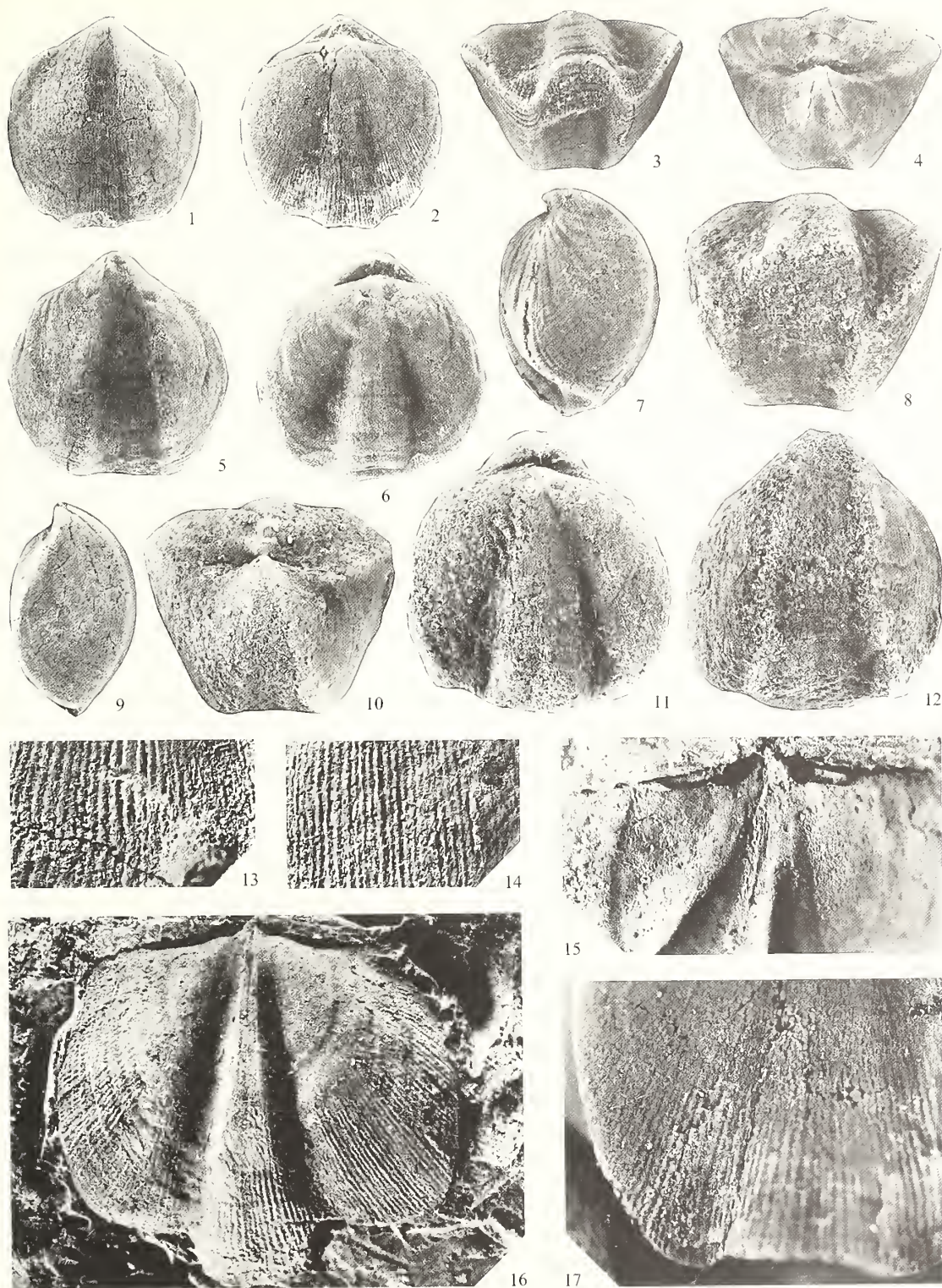
Topotype specimens of *E. sinensis* have been transversely sectioned in detail. The good preservation of the material has made it possible to reveal their internal structures as shown in Text-figures 6–7. There are no substantial differences between the brachidia of *E. sinensis* and *E. praecursor*. The number of spiralia whorls in the adult stages of *E. sinensis* and *E. praecursor* is eight to nine and three to four respectively, mainly due to the difference in shell size.

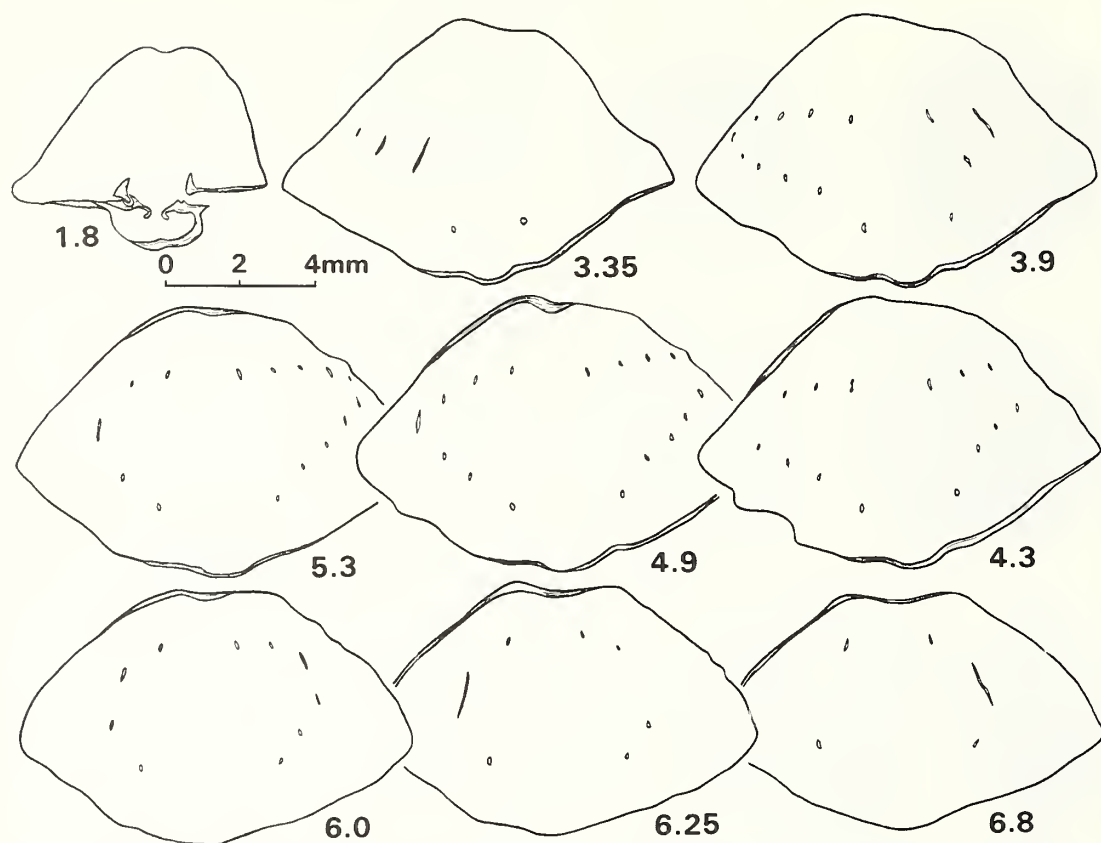
The brachidia of the early Aeronian *E. minutus* and the late Aeronian *E. songkanensis* (see Appendix) are also the same as that of the earliest taxon of the same group (for *E. minutus*, see Text-figs 8–9). All species examined herein have short but prominent jugal processes with the exceptions of *E. minutus* (8–10.5 mm wide, 7–10 mm long, and 6–8.5 mm thick), *E. songkanensis* (22.0 mm wide, 19.3 mm long, and 14.0 mm thick), and the juvenile specimen of *E. praecursor* (3.1 mm long, 2.9 mm wide and 2.2 mm thick). This is not because shell size is too small to develop the processes. The adult stages of *E. praecursor* have even smaller shells (usually only 4–5 mm, occasionally 6 mm wide) than those of *E. minutus* and *E. songkanensis* but still has well established jugal processes. Thus, features of the jugal processes may be of fundamental significance in specific classification.

A topotype specimen of *E. cinghizicus* Borisjak (see Appendix), from the Lower Llandovery of

EXPLANATION OF PLATE I

Figs 1–17. *Eospirifer praecursor* Rong, Zhan and Han, 1994. 1–12, 17, Xiazhen Formation (middle Ashgill); Zhuzhai, Yushan, north-eastern Jiangxi, East China; 1–2, 9, 17, NIGP 124755. 1, 9, ventral and lateral views of conjoined valves; $\times 8$; 2, 17, dorsal view of the valves; $\times 8$, $\times 20$ (local enlargement showing fine radial striae). 3–7, NIGP 124756; anterior, posterior, ventral, dorsal and lateral views of conjoined valves; $\times 8$. 8, 10–12, NIGP 124757; anterior, posterior, dorsal and ventral views of conjoined valves; $\times 8$. 13–16, NIGP 118704, holotype; Changwu Formation (Middle Ashgill); Pengli, Jiangshan, south-western Zhejiang, East China; 13–14, fine radial striae; $\times 20$; 15, detailed view of cardinalia; $\times 30$; 16, internal mould of dorsal valve; $\times 10$.





TEXT-FIG. 8. Serial transverse sections of one specimen of *Eospirifer minutus* Rong and Yang, 1978 (length 9.7 mm, width 11.0 mm, depth 7.4 mm); NIGP 124769 (21 sections made and 9 selected herein); Middle Xiangshuyuan Formation (lower Aeronian), Yingwuxi, Sinan, north-eastern Guizhou, South-west China.

Chinghiz, Kazakhstan, was sectioned, but unfortunately no spirallium was detected because the preservation is inadequate. Nevertheless, a pair of small jugal processes can be observed from the serial sections (Text-fig. 10). This species is characterized by a thick secondary shell having solid or very small apical cavities posteriorly in both valves, crural bases close to each other, and the two primary lamellae almost parallel.

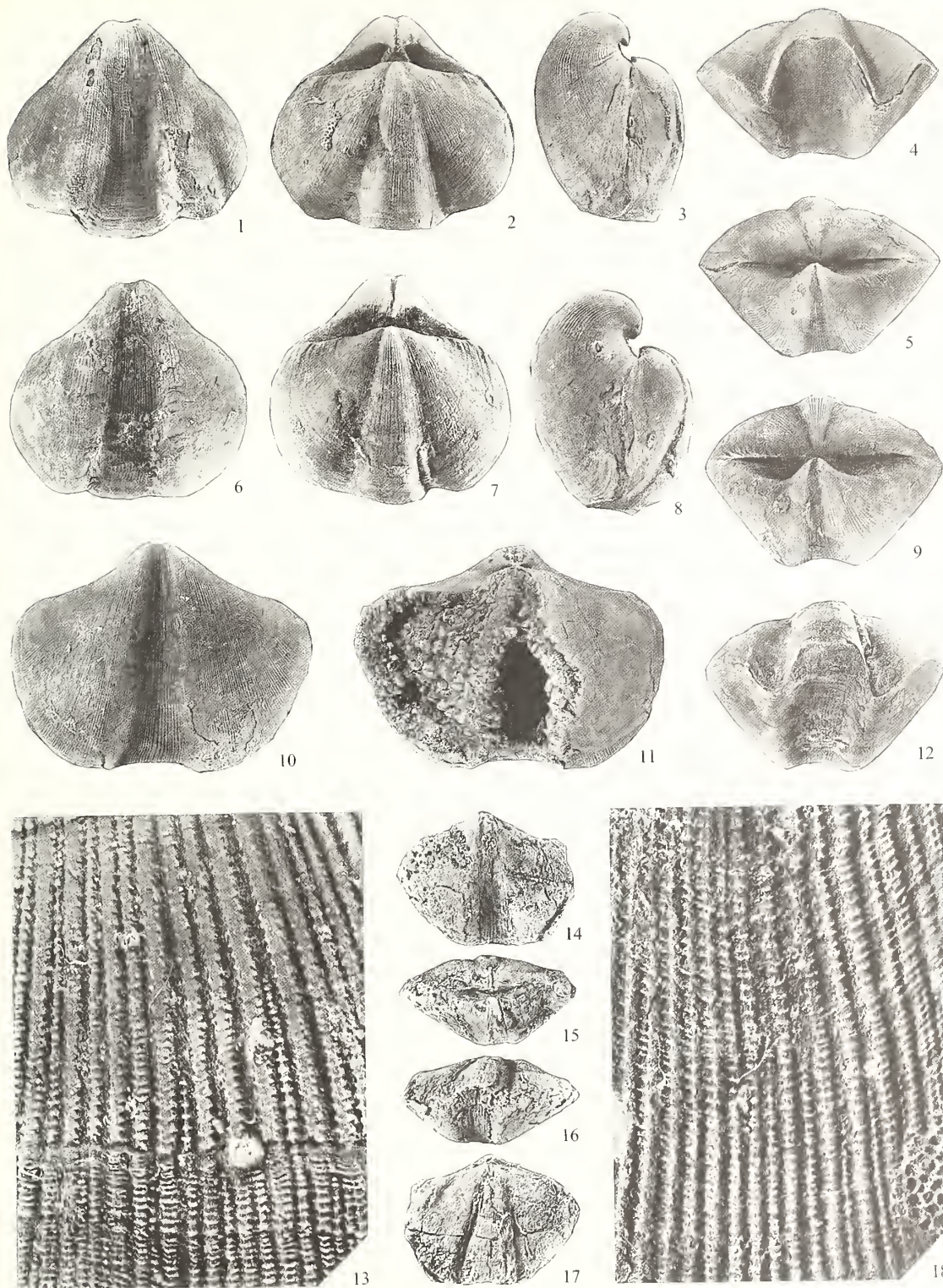
EXPLANATION OF PLATE 2

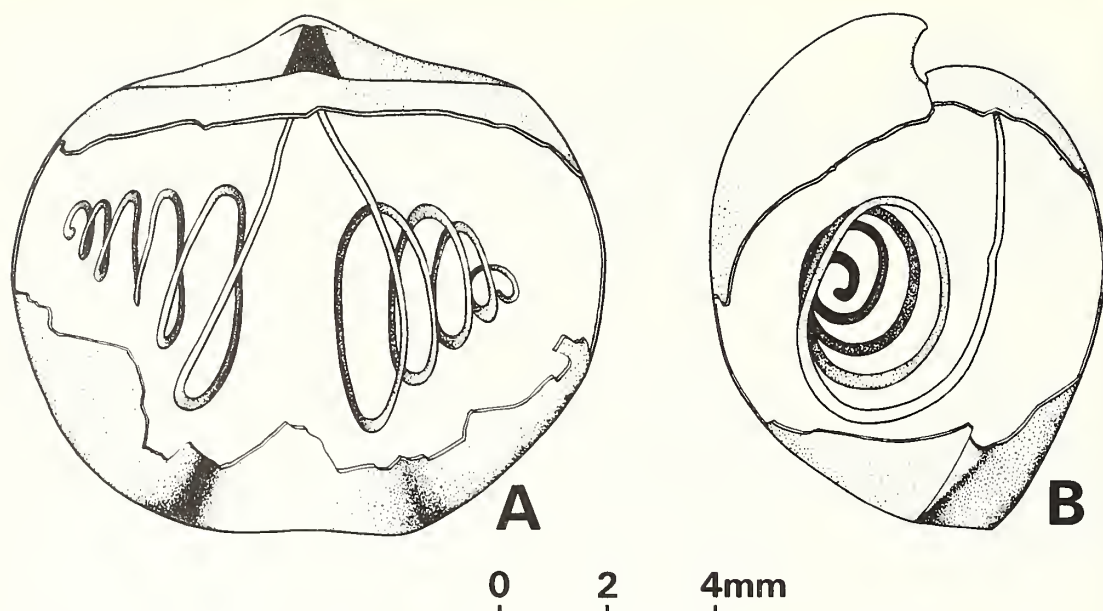
Figs 1–9, 12. *Eospirifer sinensis* Rong, Xu and Yang, 1974; Xiangshuyuan Formation (upper Rhuddanian, Lower Llandovery); Leijiatun, Shiqian, north-eastern Guizhou, South-West China. 1–5, NIGP 45215, topotype; ventral, dorsal, lateral, anterior and posterior views of conjoined valves; $\times 2$. 6–9, 12, NIGP 22302, holotype; ventral, dorsal, lateral, posterior and anterior views of conjoined valves; $\times 2$.

Figs 10–11. *Eospirifer cf. radiatus* (Sowerby); NIGP 124758; Jupiter Formation (C650) (Telychian, Upper Llandovery); Anticosti, Canada; ventral and dorsal views of conjoined valves (on the specimen in fig. 11 most of the dorsal shell is broken, showing the spirallium); $\times 1.5$.

Figs 13, 18. *Eospirifer radiatus* (Sowerby, 1834); NIGP 124759; Mulde Beds (SW16) (middle–upper Wenlock), Gotland, Sweden; detailed views of fine radial striae with concentric filae on a ventral valve (see Pl. 3, fig. 14); $\times 15$.

Figs 14–17. *Eospirifer cinghizicus* Borisiak, 1955; NIGP 124760; *Cinghizicus* Bed of Al'peiskii Horizon (Llandovery), Chinghiz, Kazakhstan; ventral, posterior, anterior and dorsal views of conjoined valves; $\times 2$.

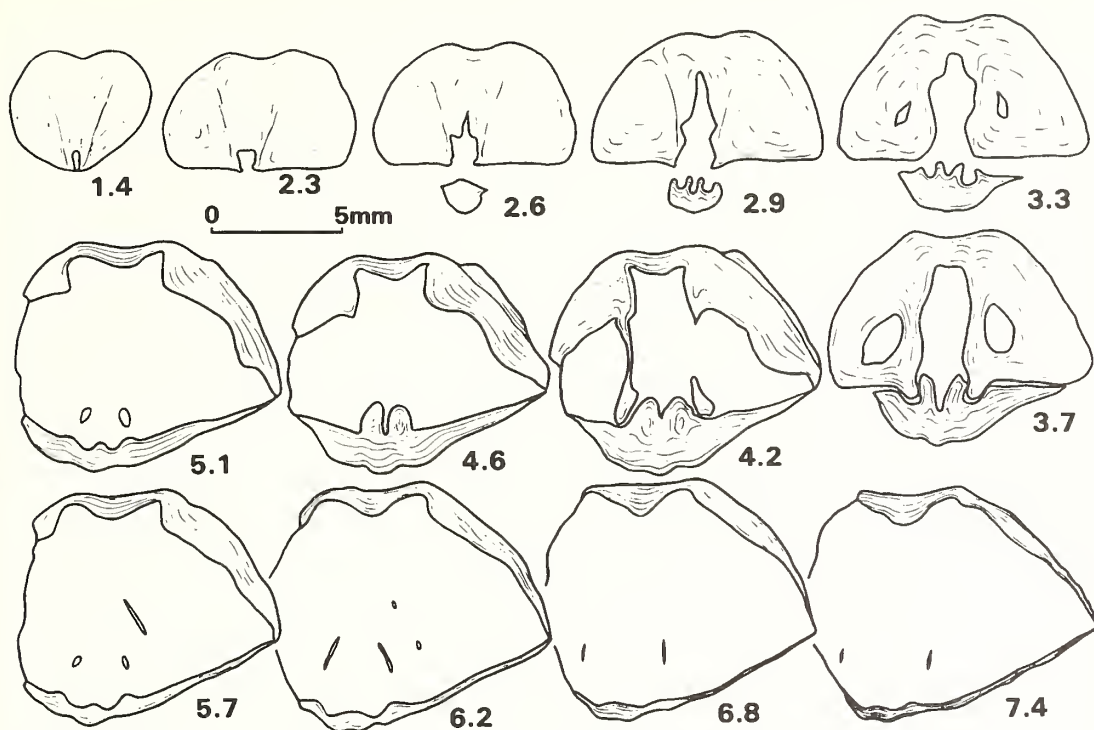




TEXT-FIG. 9. Reconstructions of brachidia of one specimen of *Eospirifer minutus* Rong and Yang, 1978; based on Text-figure 8.

The brachidium of *E. radiatus* (J. de C. Sowerby) (= *Spirifer lineatus* J. de C. Sowerby), the type species from the 'Wenlock Limestone' of Dudley, English Midlands, was described and reconstructed by St Joseph (1935, p. 322, pl. 15, fig. 10; text-figs 3–4). His description stated that 'The crural bases... continue as descending lamellae which are slightly divergent and parallel to the inner surface of the dorsal valve. There are about 7–8 whorls and the axis of the spire is directed laterally and slightly posteriorly. A jugum is in the form of a simple arch, located between two descending lamellae and about one-third of the distance from crural bases to anterior margin.' A reconstruction of the brachidium was shown in his paper (St Joseph 1935, pl. 15, figs 10, 12). No serial transverse or longitudinal sections of *E. radiatus* were published by him. Later, Boucot (1963) showed a pair of short jugal processes directed towards the interior of ventral valve at the junction of primary lamellae and crura in *E. radiatus* from the Waldron Shale, Waldron, Indiana (Boucot 1963, pl. 97, fig. 13). He also pointed out (1963, p. 687) that there is no evidence of a band connecting the jugal processes medially. This conclusion is contrary to that made by St Joseph in 1935. The contradiction has not been settled because no relevant illustrations of serial sections of eospiriferines have been published.

Two specimens of *E. radiatus* (Sowerby 1834) from the type horizon at the type locality (Text-fig. 11) and two from the Upper Wenlock of Gotland (Pl. 3, figs 1, 5, 10, 12, 14) were serially sectioned (Text-figs 12, 14). Several specimens identified as *E. cf. radiatus* (see Appendix), from the Upper Llandovery of Anticosti, were also selected for sectioning (Text-fig. 16). Reconstructions of the brachidia of British, Swedish and Canadian specimens (Text-figs 13, 15, 17) show that many features of this structure are very similar to that of *E. sinensis* (8–9 whorls of the spiralia in *E. sinensis*, and 8–13 in *E. cf. radiatus* (8 whorls) and *E. radiatus* (10 in British specimen and 13 in Swedish specimen)). It should be emphasized that a pair of ventrally acuminate processes is prominent in *E. radiatus* and *E. cf. radiatus*, and no band connecting the jugal processes medially is found. This observation is inconsistent with that of St Joseph (1935) but supports Boucot's conclusion (1963).



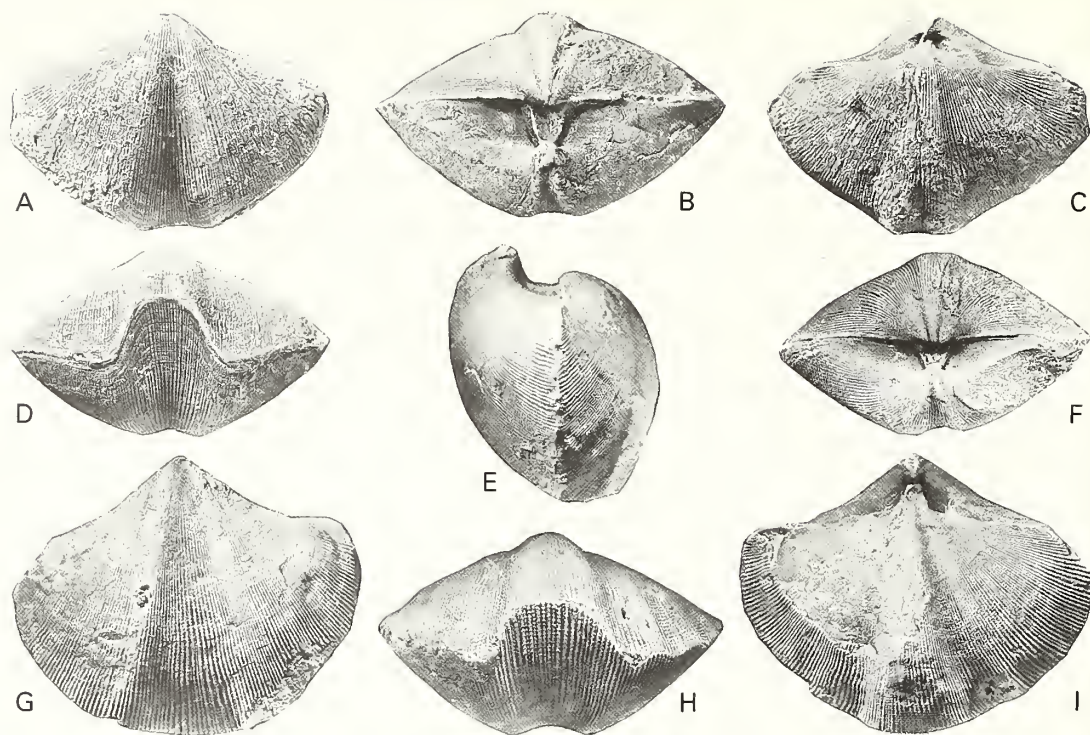
TEXT-FIG. 10. Serial transverse sections of one specimen of *Eospirifer cinghizicus* Borisiak, 1955 (length 13.1 mm, width 17.6 mm?, depth 9.9 mm); NIGP 124770 (18 sections made and 13 selected herein); Lower Llandovery Al'peisskii Horizon, Chinghiz, Kazakhstan.

In addition to *Eospirifer*, three species of *Striispirifer* (with *Hedeina*) were also sectioned to determine internal structures (see Appendix). They are topotype specimens of: (1) *S. acuminiplicatus* Rong, Xu and Yang, 1974 (Text-fig. 18; early Aeronian, Mid Llandovery), herein considered to be one of the earliest known species of *Striispirifer*; (2) *S. plicatellus* (Linnaeus, 1758; Text-fig. 20) (Wenlock) and (3) *S. yunnanensis* Rong and Yang, 1974 (Text-fig. 22; late Ludlow). Reconstructions of their brachidia are shown in Text-figures 19, 21 and 23.

The cross angles of two jugal processes at certain transverse levels (Table 1) are of significance for the general understanding of the brachidium in *Eospirifer* and for evaluating its evolution. They are at about 110–120° in the late Ordovician *E. praecursor*, 70° in earlier Llandovery *E. sinensis*, about 42° in late Llandovery *E. cf. radiatus* and 30° in Wenlock *E. radiatus* (Text-fig. 24). It should be emphasized that this reduction of the cross angles of jugal processes through the late Ordovician to Wenlock is recognized only in some species of *Eospirifer*, and not in *Striispirifer* since the cross angles are 30° in the Mid Llandovery *Striispirifer acuminiplicatus*, 80° in the Late Wenlock *S. plicatellus*, and 20° in the Late Ludlow *S. yunnanensis*. Further work on the brachidia in later *Eospirifer* (Ludlow, Přidolí, and Early Devonian) is needed.

The place, on the dorsal side of the crura, near the junction of the crura and primary lamellae, is always smooth and usually somewhat concave dorsally with no sharp geniculation (Text-figs 5, 7, 13, 15, 17, 19, 21, 23). This is probably consistent with Boucot's observation that the crus makes an obtuse angle with the primary lamellae in *Cyrtia*, *Eospirifer*, *Janius*, and *Striispirifer* (Boucot 1963).

With regard to the discussion above, it is verified that a pair of small, centro-ventrally acuminated jugal processes was well-established in the Ashgill and well-developed in most of the Silurian

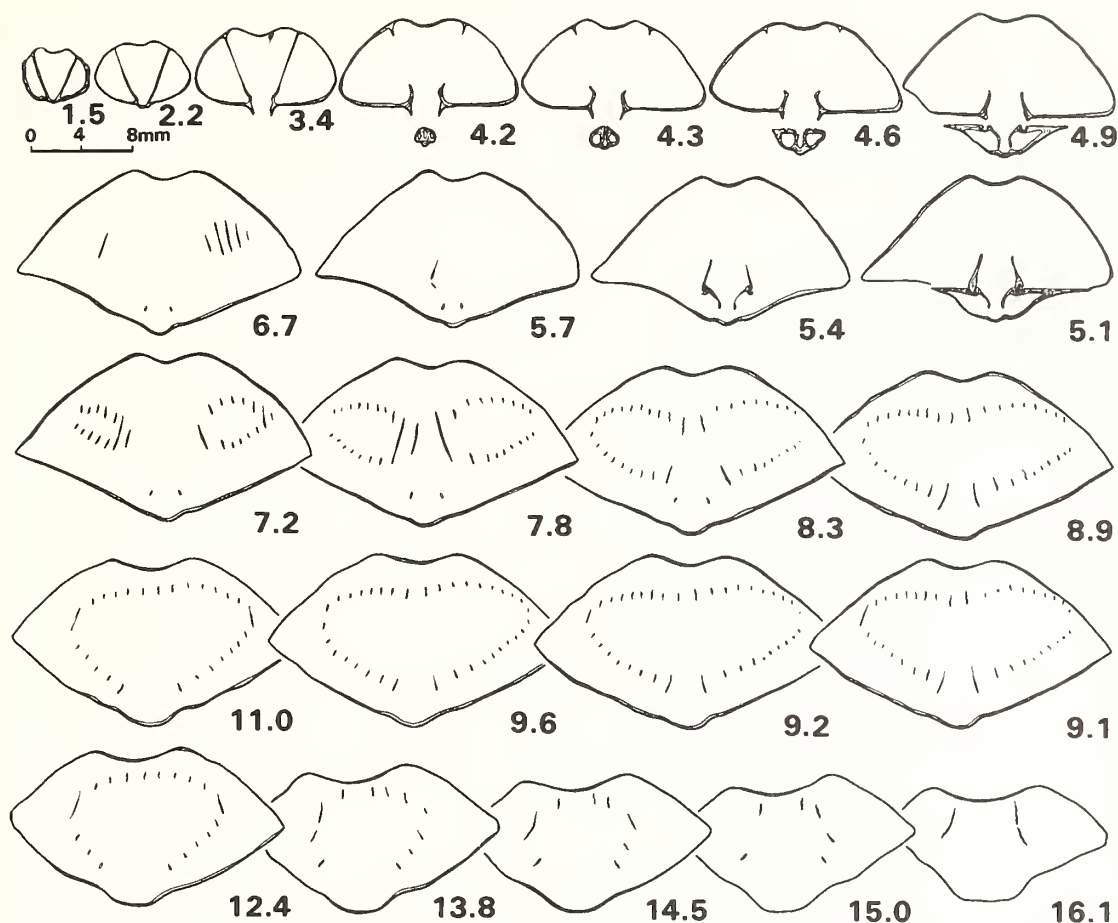


TEXT-FIG. 11. Topotypes of *Eospirifer radiatus* (Sowerby, 1834). A, C, D, F, NIGP 124758a; ventral, dorsal, anterior and posterior views of a conjoined shell; $\times 1.5$, B, E, G-I, NIGP 124759a, posterior, lateral, ventral, anterior and dorsal views of a conjoined shell which has been sectioned for this paper (see Text-figs 12-13); $\times 2$. Much Wenlock Limestone Formation (uppermost Wenlock), Dudley, West Midlands, England.

eospiriferines. No jugum has been found in any specimen of eospiriferine examined herein. It seems unlikely that there was an uncalcified jugum between the two jugal processes. The processes would connect with each other and become a jugum in much later forms of some species in the *Spirifer* group (such as advanced stocks in the Devonian and later). Therefore the form of the brachidium was probably stable during the evolution of the eospiriferines.

Measurements (Table 2; for definitions see Text-fig. 15) of various distances and proportions show: (1) T_1/T is within the range of 98-100 per cent. in different species, with the exception of 95.7 per cent. in a juvenile specimen of *Eospirifer praecursor* (2.9 mm in shell width). We assume this value was significantly stable in the adult stages of many species of eospiriferines. It means that the level of jugal process is located approximately at the level of maximum shell thickness; (2) T_2/T_1 is variable in different taxa (24-41.2 per cent., with the exception of 15 per cent. in a juvenile specimen of *Eospirifer praecursor*) and the value depends on the degree of development of jugal process; (3) L_2/DL is remarkably stable in different species, since all are close to each other within the range 77-87 per cent. (usually 80-85 per cent.), with the exception of 61 per cent. in a juvenile specimen of *Eospirifer praecursor*. The smaller proportion of L_2/DL in the pre-adult stage indicates that it has a significantly smaller lophophore apparatus; (4) L_1/DL is variable in different species, but always within the range 33-45 per cent.

One of the interesting features of this study is the strong asymmetry commonly shown by the spiralia. This asymmetry is much greater than that shown by the shell exteriors. The preservation of most specimens studied is perfect which makes it unlikely that any post mortem mechanical

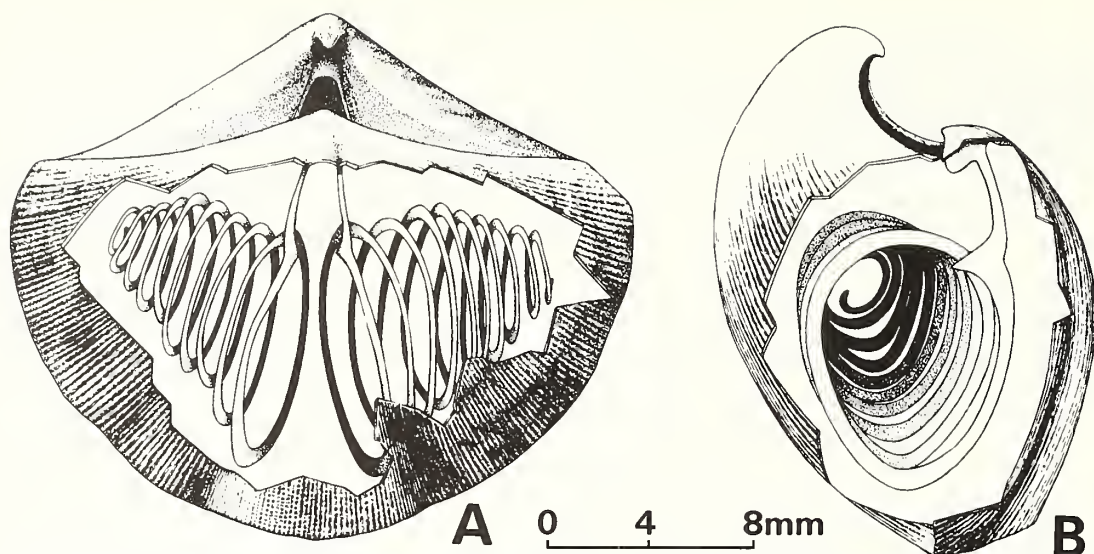


TEXT-FIG. 12. Serial transverse sections of a toptype specimen of *Eospirifer radiatus* (Sowerby, 1834) (length 19.3 mm, width 24.2 mm, depth 7.45 mm); NIGP 124759a (37 sections made and 24 selected herein); same locality and horizon as for Text-figure 11.

distortion resulting from deformation of the entombing sediments is involved. The state of the complete shells excludes the possibility that asymmetry was due to mechanical injury during life because there is no damage to the shells. Elliott (1958) recognized 'a congenital defect of brachial development', but it can not be proved in fossils, and we agree with Ager and Riggs (1964) that gross distortion of the spiralia would have a harmful effect on a brachiopod's feeding mechanism. Therefore, the asymmetry of the spiralia in eospiriferines is normal and common, and may be seen in the other stocks of the *Spirifer* Group.

COMPARISONS OF EARLY EOSPIRIFERINES WITH OTHER RELATED GROUPS

The early eospiriferines include some of the species assigned to *Eospirifer* and *Striispirifer* (= *Hedeina* Boucot, 1963) known from the upper Ordovician and Lower Silurian (Llandovery). The species attributed to the Early-Mid Llandovery genera, *Yingwuspirifer* Rong, Xu and Yang, 1974, and *Espella* (= *Laewispirifer* Ushatinskaya, 1977), are not discussed herein since no toptype material of these taxa was available for serial sectioning. Material of the type species of the Ashgill genus *Iliella* Rukavishnikova (assigned to the eospiriferines by Nikitin *et al.* 1980) was serially



TEXT-FIG. 13. Reconstruction of brachidia of one specimen of *Eospirifer radiatus* (Sowerby, 1834); based on Text-figure 12.

transversely sectioned for this paper but no brachidium was found. However, it seems to the present authors that *Iliella* may be rejected from the eospiriferines because typical early atrypoid cardinalia are present and there is no real ventral interarea on the topotypes of the type species, *Iliella minima* Rukavishnikova, 1980.

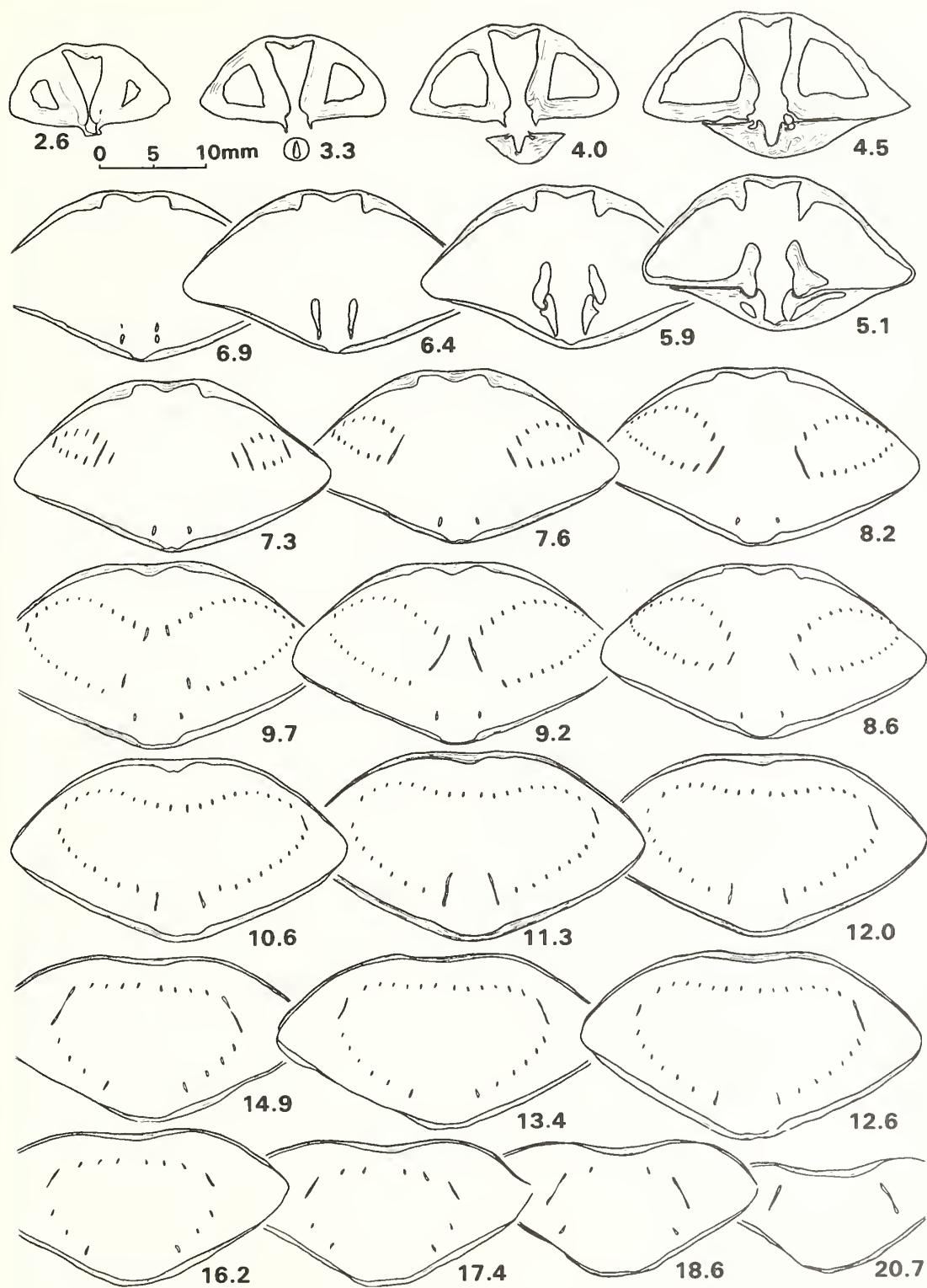
Early atrypoids

Although the study of the ontogenetic development of spiralia in eospiriferines is difficult, characters of the brachidium can still be compared with those of the other early spire-bearing groups (atrypoids and athyroids) of the later Ordovician.

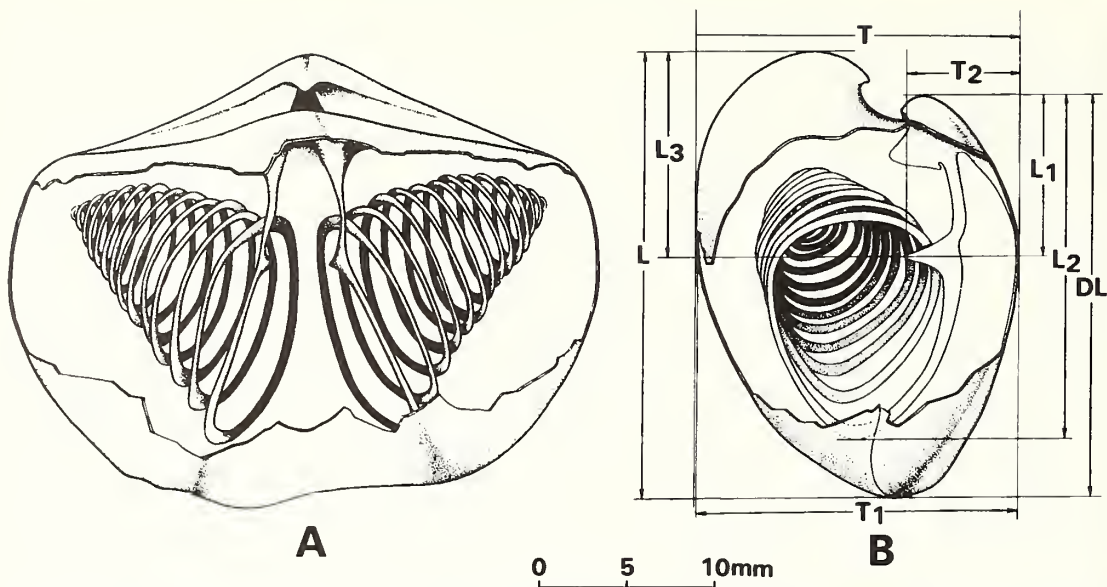
A comprehensive study of the spiralia of Caradoc and Ashgill atrypoids was made by Copper (1986). It revealed that the spiralia of Caradoc genera (such as *Manespira* Copper, 1986; *Protozyga* Hall and Clark, 1893; *Idiospira* Cooper, 1956) were primitive and varied. The spiralia of Ashgill genera (such as *Anazyga*, *Zygospira*, *Catazyga*, and *Eospirigerina*) were more complicated, and usually possessed a complete, single-structure, either U-shaped or W-shaped jugum with common features: small and simple spiralia, with their cones directed medially or dorso-medially in fewer whorls. Generally, they have a simple jugum located between the divergent crura in most representatives of the atrypoids. However, *Cyclospira* Hall and Clark, 1893, one of the early atrypoids, ranging from late Caradoc to Ashgill, is an exception (Copper 1986). It is important to compare the brachidium of *Cyclospira* with that of the earliest representatives of eospiriferines since, among all atrypoid genera it is the brachidium of *Cyclospira* that most resembles that of the earliest eospiriferines. We may take two taxa as examples for comparison, *Cyclospira bisulcata* (Emmons, 1842) from the Trenton Limestone (the type horizon is latest Caradoc or earliest Ashgill; Copper 1986) and *Eospirifer praecursor*, the earliest known eospiriferine (mid Ashgill).

The morphology of the crus and brachidium show an essential difference between the two species: the spiralia are directed centrally in *C. bisulcata* (Text-fig. 25, following text-fig. 2 of Copper 1986),

TEXT-FIG. 14. Serial transverse sections of one Swedish specimen of *Eospirifer radiatus* (Sowerby, 1834) (length 24.5 mm, width 32.6 mm, depth 17.5 mm); NIGP 124771 (66 sections made and 24 selected herein); Mulde Beds (SW16) (middle-upper Wenlock), Gotland, Sweden.



TEXT-FIG. 14. For caption see opposite.



TEXT-FIG. 15. Reconstruction of brachidia of one Swedish specimen of *Eospirifer radiatus* (Sowerby, 1834); based on Text-figure 14.

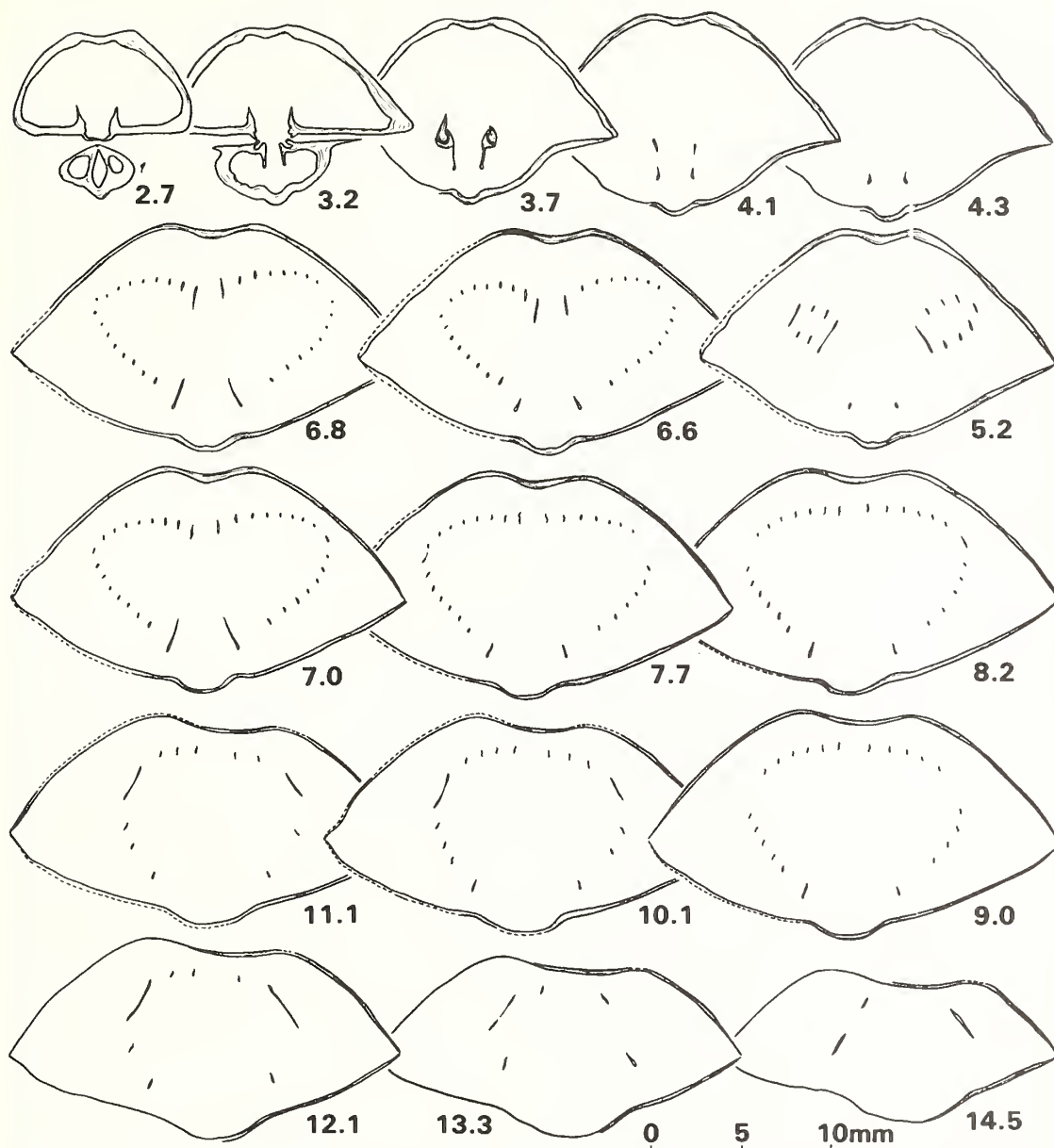
but laterally in *E. praecursor*. The spiralium is located between two crura in *C. bisulcata*, but outside them in *E. praecursor*; a pair of very small jugal processes is present in *E. praecursor*, but absent in *C. bisulcata*. The differences are so fundamental that these taxa have been assigned to different orders.

There are, however, some remarkable differences between the brachidium of *Cyclospira* and that of other early atrypoid taxa (Copper 1986). One of the most important characters is that the junction between crura and primary lamellae is sharply geniculate in many of the Ordovician smooth or ribbed atrypoids, but is not sharply geniculated in *Cyclospira*. Many early atrypoids have different types of juga, whereas *Cyclospira* has no jugum (Copper 1986, p. 831). Furthermore, it is surprising that some features of the brachidium in *C. bisulcata* are also similar to that of *E. praecursor*, for example: (1) the very small size of the spiralium; (2) the few whorls (one to four) of the spiralium; (3) the slightly divergent crura (with an angle of about 50°) and anteriorly continuous with primary lamellae; (4) the crura is arched ventrally to varying degrees; (5) the junction between crura and primary lamellae is not sharply geniculated; (6) the crura and primary lamellae are located near and parallel to the inner surface of the dorsal valve; (7) the absence of a jugum.

Although some of the similarities mentioned above are probably due to strong similarities in shell size, form and outline (compare Copper 1986, pl. 74, figs 7–21 with Pl. 1, figs 1–12), it seems to us that they are significant in any discussion and evaluation of the origin of the eospiriferines (see below).

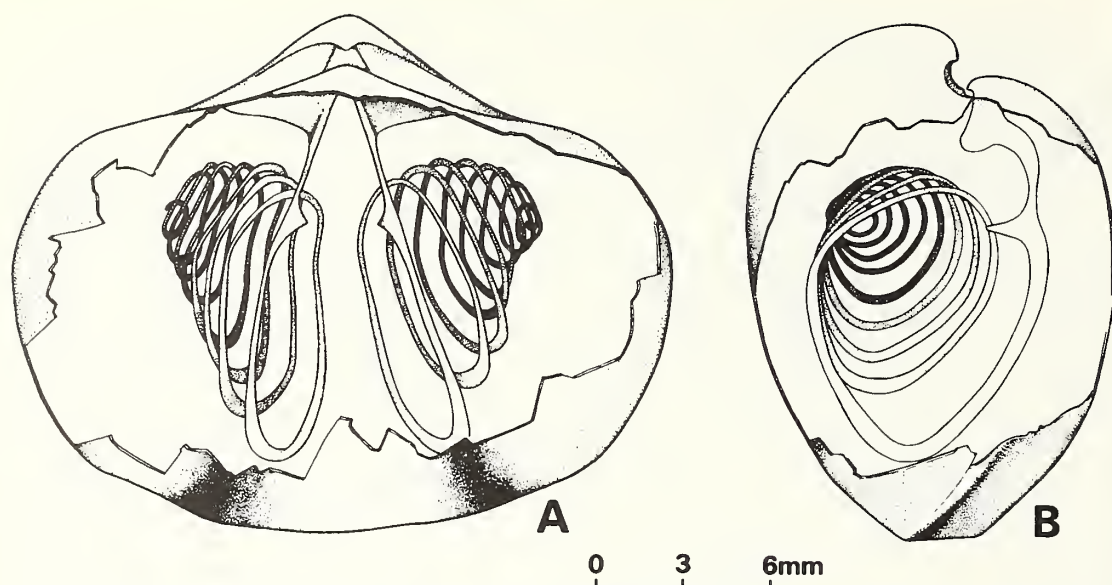
Early athyroids

Some of the early athyroids are well-known in pre-Silurian rocks in many places in the world. They are *Hindella* Davidson, 1882, *Cryptothyrella* Cooper, 1942 and *Whitfieldella* Hall and Clark, 1893, known to make their first appearance in the middle Ashgill. Their brachidia are more complex than those of early atrypoids and the brachidia of *Hindella* and *Cryptothyrella* are composed of laterally directed spiralia and a relatively complicated jugum. They are evidently different from *Eospirifer praecursor* in all respects, including the orientation and location of the brachidia.



TEXT-FIG. 16. Serial transverse sections of one specimen of *Eospirifer* cf. *radiatus* (Sowerby, 1834) (length 17.7 mm, width 21.2 mm, depth 12.6 mm); NIGP 124772 (33 sections made and 17 selected herein); Jupiter Formation (Upper Llandovery), Anticosti.

A primitive but poorly known athyroid is *Apheathyris* Fu, 1982, from the topmost part of the Pingliang Formation (upper Caradoc), Shijiezigou, Guyuan, Ningxia, North China. It is characterized externally by having a large shell (30 mm long and 29 mm wide), a ventri-biconvex lateral profile and a smooth shell surface. Fu (1982, p. 172, text-fig. 84) made serial sections of a single specimen (the holotype) of *A. guyuanensis* Fu, 1982, the type species of the genus. The sections show that there are small, short, separate socket plates, laterally oriented spiralia with about 11



TEXT-FIG. 17. Reconstruction of one specimen of *Eospirifer* cf. *radiatus*; based on Text-figure 13.

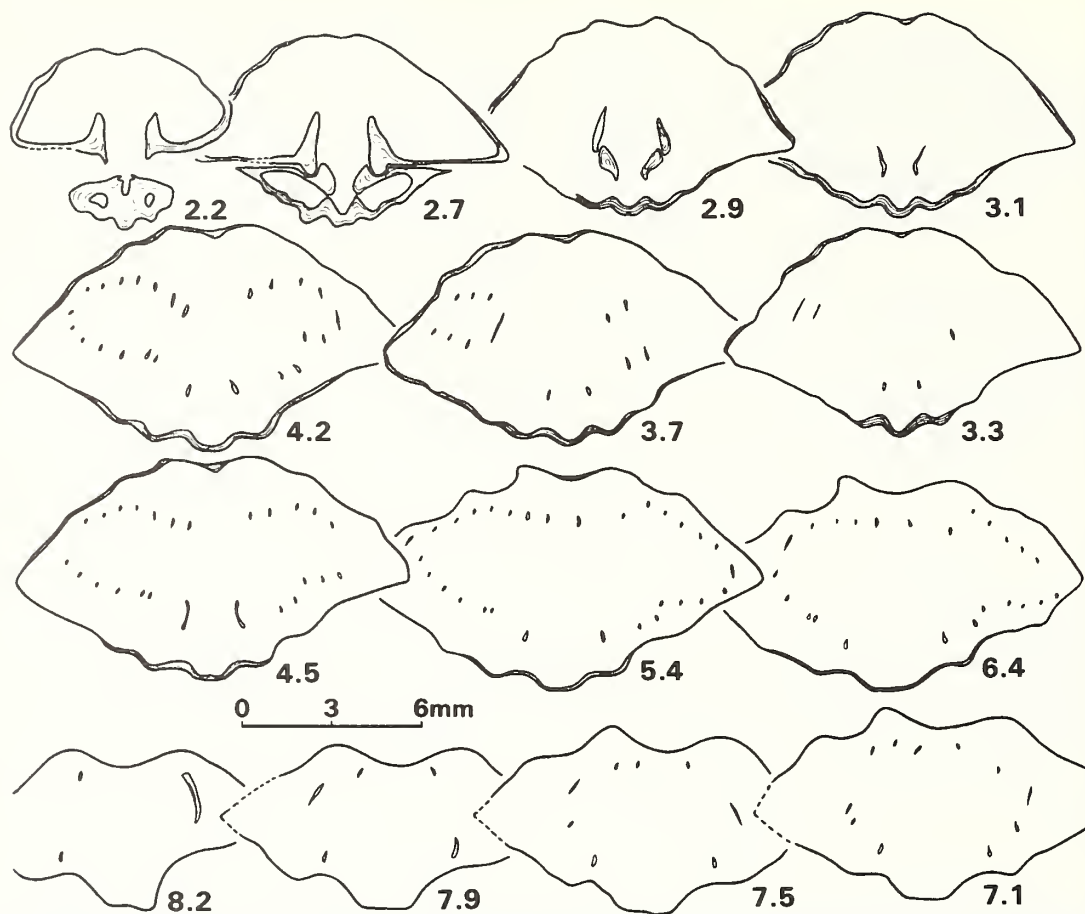
whorls, a complicated jugum(?), but no dental plates. Unfortunately, the nature of the jugum and its relationship with the spiralia are unknown. Nevertheless, the internal structures of *Apheathyris* and *Eospirifer* are so fundamentally different that it is reasonable to suppose that the earliest eospiriferines were not derived from the athyroids.

The earliest and poorly known athyroid(?) is *Weibeia* Fu, 1983, from Jinghe Formation (lower Caradoc), Dongzhuang, Liquan, Shaanxi Province, North China. It was assigned to the Meristellidae by Fu (1982, p. 171). This genus possesses a pair of parallel dental plates in the ventral valve and 'brachial plates' in the dorsal valve. However, the assignment of *Weibeia* to the meristellids or other groups is still uncertain since the brachidium of *W. spiriferoides* Fu, 1982, type species of this genus, is unknown and a reliable comparison of the brachidia between *Weibeia* and *Eospirifer* cannot be made at present.

EXPLANATION OF PLATE 3

- Figs 1, 5, 10, 12, 14. *Eospirifer radiatus* (Sowerby, 1834); NIGP 124759; same locality and horizon as Pl. 2, figs 13, 18; posterior, anterior, dorsal, lateral and ventral views of conjoined valves; $\times 1.5$.
 Figs 3-4, 9, 13, 15, 17, 19-20. *Eospirifer* cf. *radiatus* (Sowerby); same locality and horizon as Pl. 2, figs 10-11. 3-4, 9, 13, 17, NIGP 124761; lateral, dorsal, ventral, posterior and anterior views of conjoined valves, $\times 1.5$. 19, enlargement of posterior part of same specimen in dorsal view showing a complete deltidium; $\times 8$. 15, 20, NIGP 124758; lateral view of conjoined valves and enlargement of posterior part of dorsal view showing a complete deltidium; $\times 1.5$, $\times 8$.
 Figs 2, 6, 8, 11, 18. *Eospirifer songkanensis* Wu, 1978; NIGP 124762; topotype; upper part of Shihniulan Formation (upper Aeronian, Middle Llandovery); Hanjiadian, Songkan, Tongzi, north Guizhou, South-west China; lateral, posterior, dorsal, ventral and anterior views of conjoined valves; $\times 1.5$.
 Figs 7, 16. *Eospirifer praecursor* Rong, Zhan and Han, 1994; same locality and horizon as Pl. 1, figs 1-12. 7, NIGP 124755; posterior view of conjoined valves; $\times 8$. 16, NIGP 124757; lateral view of conjoined valves; $\times 8$.





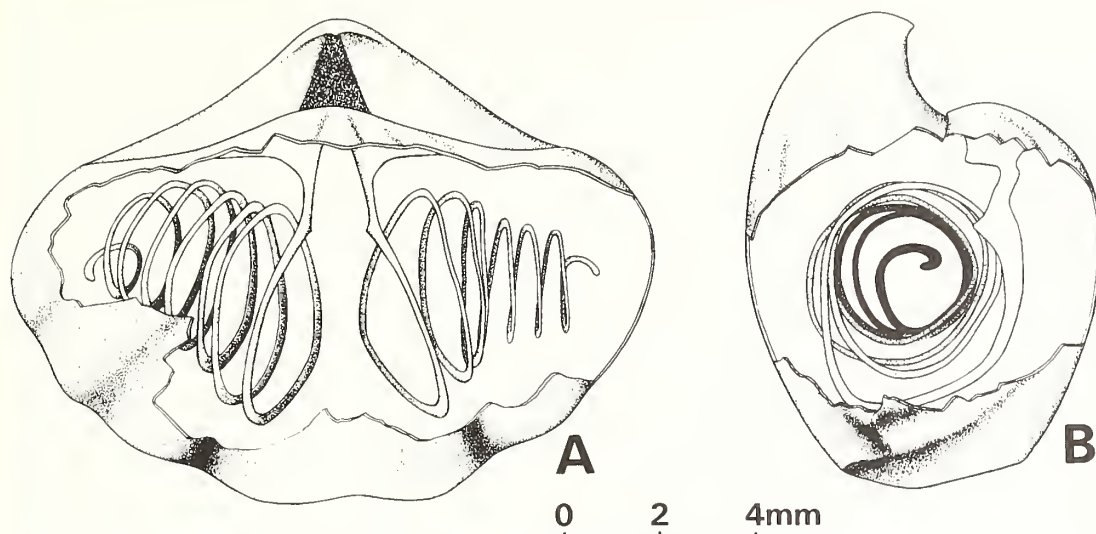
TEXT-FIG. 18. Serial transverse sections of one specimen of *Striispirifer acuminiplicatus* Rong, Xu and Yang, 1974 (length 9.8 mm, width 13.35 mm, depth 7.45 mm); NIGP 124773 (31 sections made and 14 selected herein); Middle Xiangshuyuan Formation (lower Aeronian, Middle Llandovery), Leijiatun, Shiqian, north-eastern Guizhou, South-west China.

DISCUSSION AND CONCLUSIONS

Origin of the eospiriferines

Morphological changes in the cardinalia during the ontogeny of *E. praecursor* led Rong *et al.* (1994) to consider the possibility that the oldest known eospiriferines were derived from an atrypoid stock; a potential ancestor of the eospiriferines could not be identified because of inadequate material (only external and internal moulds were studied). The new material (a large number of conjoined valves) of *E. praecursor* sectioned for this paper now makes it possible to ascertain the nature of its brachidium for further evaluation of the origin of this group.

The microsculpture of *E. praecursor* is of striations so fine that the shell surface often appears to be smooth. The shell size and shape of *E. praecursor* (Pl. 1, figs 1–17) are evidently similar to those of *Cyclospira bisulcata* (compare Copper 1986, pl. 74, figs 7–21). There are also strong similarities between their brachidia, suggesting a closer relationship. In particular, the spiralium of the early growth stages of *E. praecursor* is much more similar to that of the adult stages of *C. bisulcata* than to that of any other known atrypoid genus, although it does not mean that the former must have evolved from the latter.

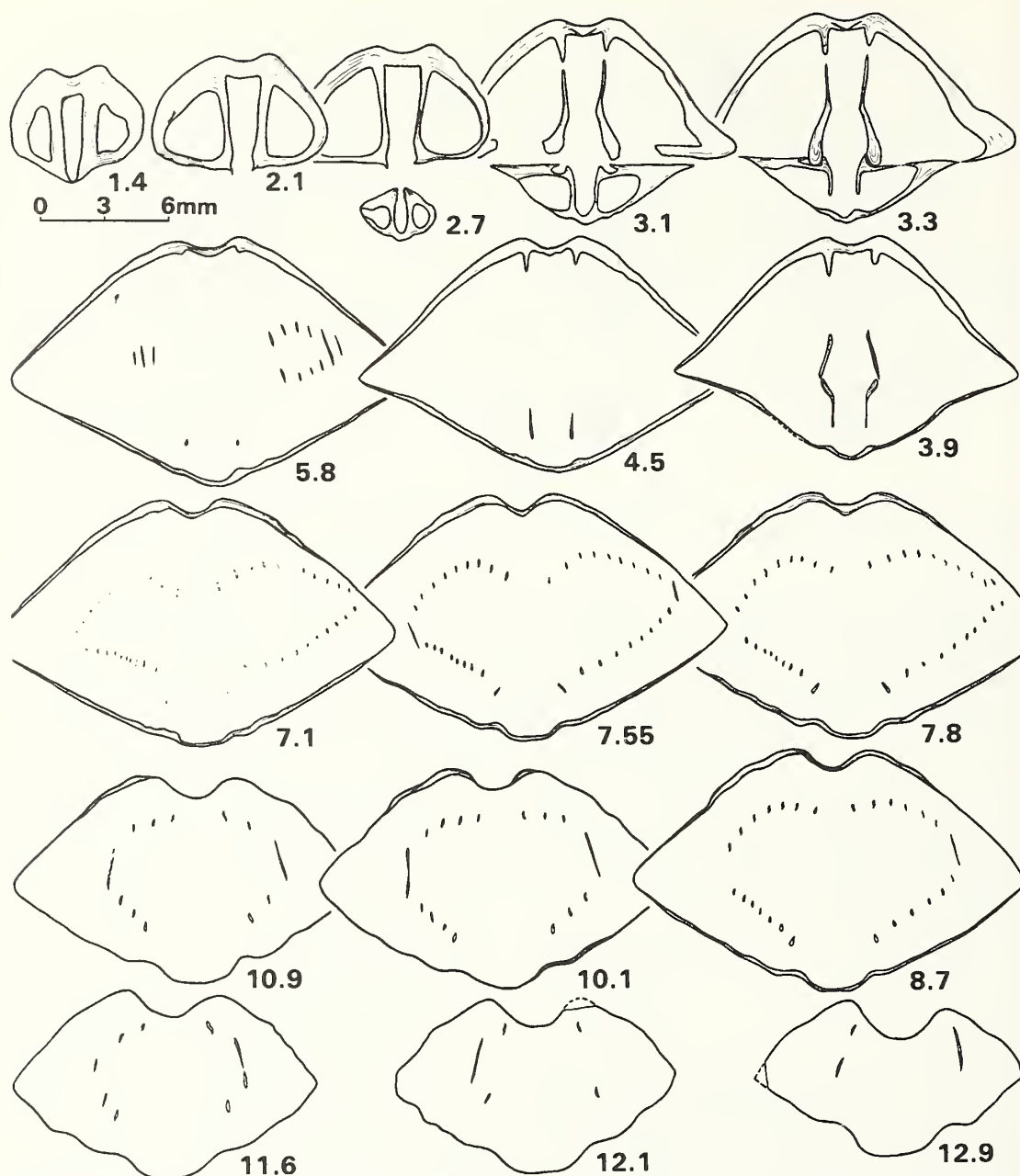


TEXT-FIG. 19. Reconstruction of brachidia of one specimen of *Striispirifer aciminiplicatus* Rong, Xu and Yang, 1974; based on Text-figure 15.

Based on the discussion above, it seems to us that the eospiriferines may have originated from an unknown atrypoid ancestor possessing a centrally directed spiralium. The strophic condition was probably a secondary development accompanying the eversion of the lophophore and the rotation of its arms and their brachidial supports (Williams and Hurst 1977, p. 107). In a population of a *Spirifer* Group species from the Lower Devonian rocks in western Junggar, north-western Xinjiang, Hou Hong-fei, Xu Han-kui and Rong Jia-yu observed in 1990 that larger individuals have, but smaller ones lack, well-developed interareas. Thus the absence and presence of well-defined interareas can occur in different growth stages of the same population of the same species. Therefore, *E. praecursor* may have originated from such atrypoids, as the shells grew to accommodate spiralia spaces changing direction from centrally to laterally. *Eospirifer* and *Cyclospira* might have shared a common ancestor from which *Cyclospira* originated first and *Eospirifer* later, independently.

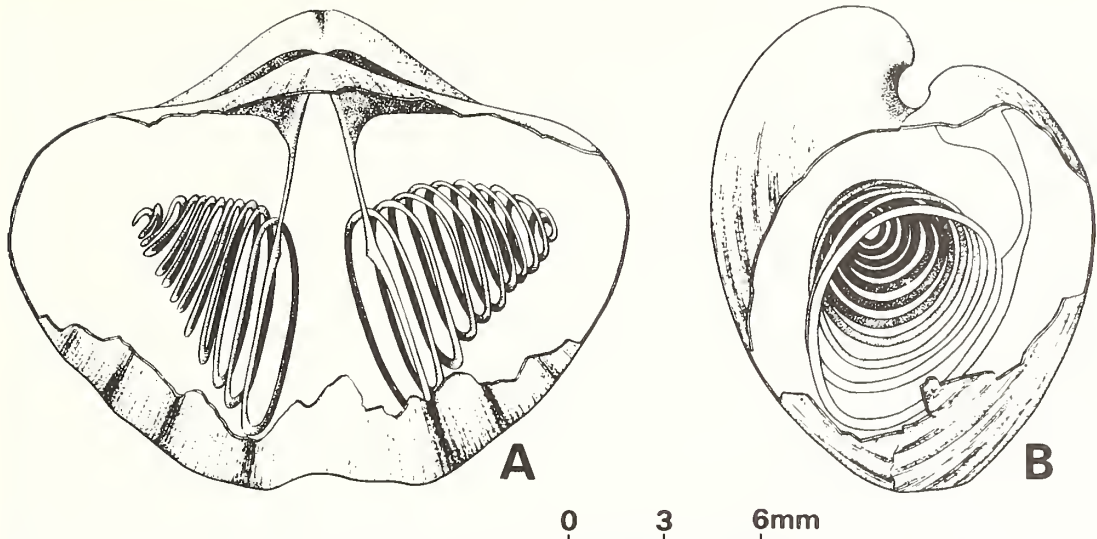
Discovery of a striated cardinal process in the type species of Eospirifer

The attachment area for the dorsal diductor scars of the eospiriferines was regarded as smooth (Boucot 1963, p. 684), and this feature was considered to be one of the most important bases for the recognition of the eospiriferines (Pitrat 1965, p. H668). The presence of a striated cardinal process has been used for tracing the genera of the group by some authors. *Endospirifer* of Ludlow age (Tachibana, 1981, p. 36) and Cyrtiidae gen.? et sp. nov. of early Ludlow age (Strusz 1984, pp. 125, 140), very similar to *Eospirifer* and *Striispirifer* (with *Hedeina*) respectively, have been defined based on this character; a new cyrtiid genus, *Hedeinopsis* Gourvennec, 1990, more or less like *Striispirifer*, has been established in terms of a striated cardinal process, a delthyrial plate and a deltidial cover. Before 1980, however, some species of the eospiriferines e.g. *Eospirifer*, *Striispirifer*, *Janius*, *Nikiforovaena* and *Cyrtia*, in which a striated cardinal process occur, had been described by Gratsianova (1967, p. 119), Kul'kov (in Alekseeva et al. 1970, p. 143, text-fig. 83; p. 146, text-fig. 85; p. 149, text-fig. 87), Ivanova (1971, p. 45, pl. 6, figs 4–5, 7), and Rong and Yang (1978, pp. 363–365, text-figs 4–6; pl. 2, figs 23–24, pl. 3, fig. 30). Based on the Chinese material, moreover, Rong and Yang (1978, pp. 364–365) pointed out that (1) the Rhuddanian–Aeronian (Early–Mid Llandovery) eospiriferines e.g. *Eospirifer*, *Yungwuspirifer* and *Striispirifer*, bear a smooth area for diductor attachment at the posterior end of the dorsal valve; (2) *Striispirifer* sp. in the early



TEXT-FIG. 20. Serial transverse sections of one specimen of *Striispirifer plicatellus* (Linnaeus, 1758) (length 15.0 mm, width 19.7 mm, depth 11.9 mm); NIGP 124765 (39 sections made and 17 selected herein); Much Wenlock Limestone Formation (Upper Wenlock), England.

Telychian (Late Llandovery) possesses rare and fine ridges in the attachment area, indicating an embryonic form of the striated cardinal process; and (3) many species of *Eospirifer*, *Striispirifer* and *Xinanospirifer* in the late Telychian (Late Llandovery) have a well-established striated cardinal



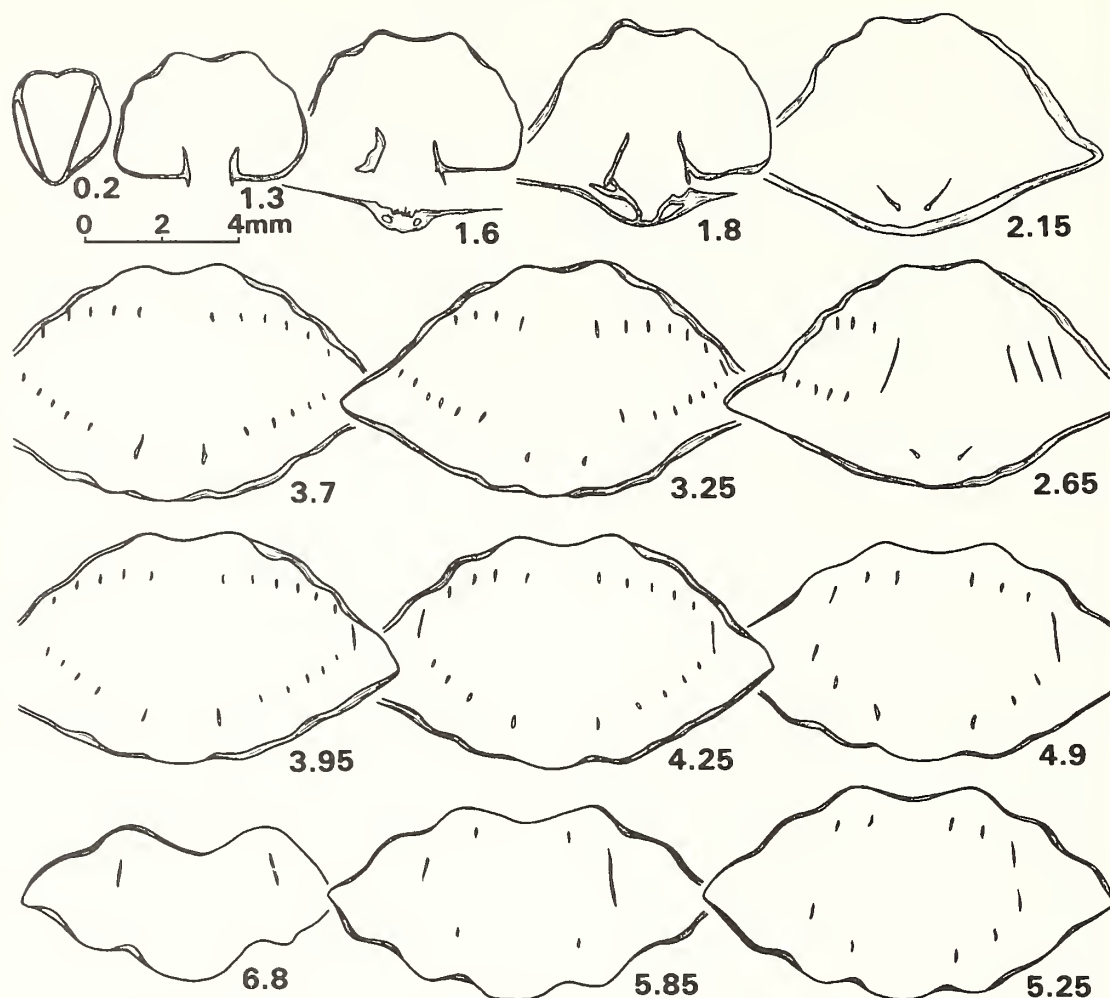
TEXT-FIG. 21. Reconstruction of one specimen of *Striispirifer plicatellus* (Linnaeus, 1758); based on Text-figure 17.

process. This suggests an evolutionary trend within the early eospiriferines. Re-examination of the topotype specimen of the type species of *Eospirifer*, *E. radiatus* (Sowerby) of Wenlock age, re-examined and serially sectioned in this paper, demonstrates that it does possess a comb-like cardinal process (Text-fig. 26). All facts mentioned above indicate that the area for diductor attachment of dorsal valve in the eospiriferines may or may not be comb-like. Thus, the presence or absence of such a cardinal process cannot be regarded as one of the most important and distinctive features in the generic classification of the group.

Evolution of the eospiriferines

The most significant innovations in anatomical design of the *Spirifer* Group at the outset of its history include: (1) a well-developed interarea; (2) a wider and straight hinge-line; (3) a well-defined dorsal fold; (4) fine radial microsculpture; (5) spiralia directed ventro-laterally; and (6) a pair of small jugal processes. The present data and those of Rong *et al.* (1994) indicate that these large-scale evolutionary changes, i.e. early experimentations, were generated during the mid Ashgill (late Ordovician), when the earliest eospiriferines (such as *E. praecursor*) made their first appearance. Subsequently, all of these evolutionary novelties were firmly stabilized probably in all later eospiriferines. They remained stable for more than 50 million years and this can be recognized as a period of evolutionary stasis within the eospiriferines. Thus, these animals seem to have undergone early experimentation in the Late Ordovician and then stabilization later during the Silurian to Mid Devonian.

The general morphology of the skeletal apparatus supporting the lophophores in eospiriferines differs more or less in size and shape, but is basically immutable as regards rotation. The junction between the crura and primary lamellae is smooth and concave ventrally, and a pair of very small jugal processes is present in *E. praecursor*. This is the case with the later taxa studied here, which lack a jugum between the two crura. Once this character was established in the Ashgill species of eospiriferines, there were no remarkable changes in this character until some time during the Devonian, with the exception of the shape of crura: arched ventrally in *E. praecursor* (see Text-fig. 4A, 1.5; 4B, 2.45), but flat in later taxa of eospiriferines (see Text-fig. 6, 8.6). The jugal process in the earliest eospiriferines represents an evolutionary novelty that appeared before the late Ordovician mass extinction event.

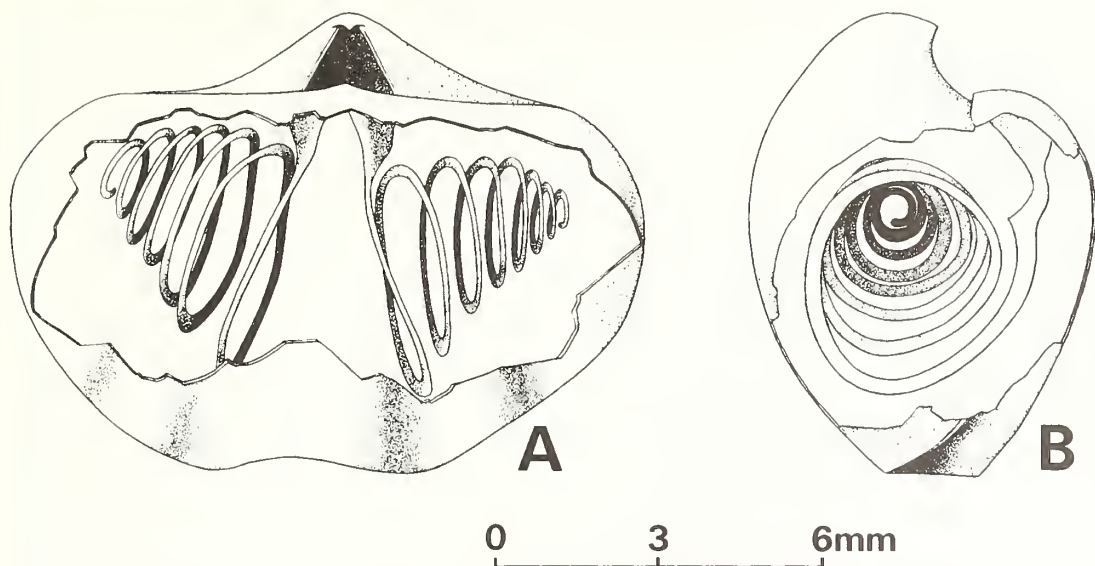


TEXT-FIG. 22. Serial sections of one specimen of *Striispirifer yunnanensis* Rong and Yang, 1978 (length 8.3 mm, width 11.8 mm, depth 6.5 mm); NIGP 124774 (21 sections made and 14 selected herein); Kuanti Formation (Upper Ludlow), Qujing, eastern Yunnan, South-west China.

Almost all large-scale evolutionary innovations occurred immediately after the appearance of the *Spirifer* Group except for the development of crural plates, which probably occurred at the beginning of the Llandovery (the *acuminatus* Biozone). Late Ordovician *E. praecursor* appear to possess no crural plates (Rong *et al.* 1994), whereas *E. tasmaniensis* (Sheehan and Baillie, 1981), from the earliest Silurian, and all other later species of eospiriferines have crural plates. *E.?* sp. (Sheehan and Baillie 1981), from the Arndell Sandstone at Locality F2, Westfield Quarr, Tasmania, is from strata corresponding to the latest Ordovician *persculptus* Biozone (Rong *et al.* 1994) but it is unknown whether it has the crural plates since no dorsal interior of this undetermined species is recorded.

Dispersal of early eospiriferines and their biogeographical significance

Eospirifer is known to be both a Lazarus and successive progenitor taxon which made its first appearance in Asia (East China and ?Kazakhstan) in the mid Ashgill; it disappeared in the

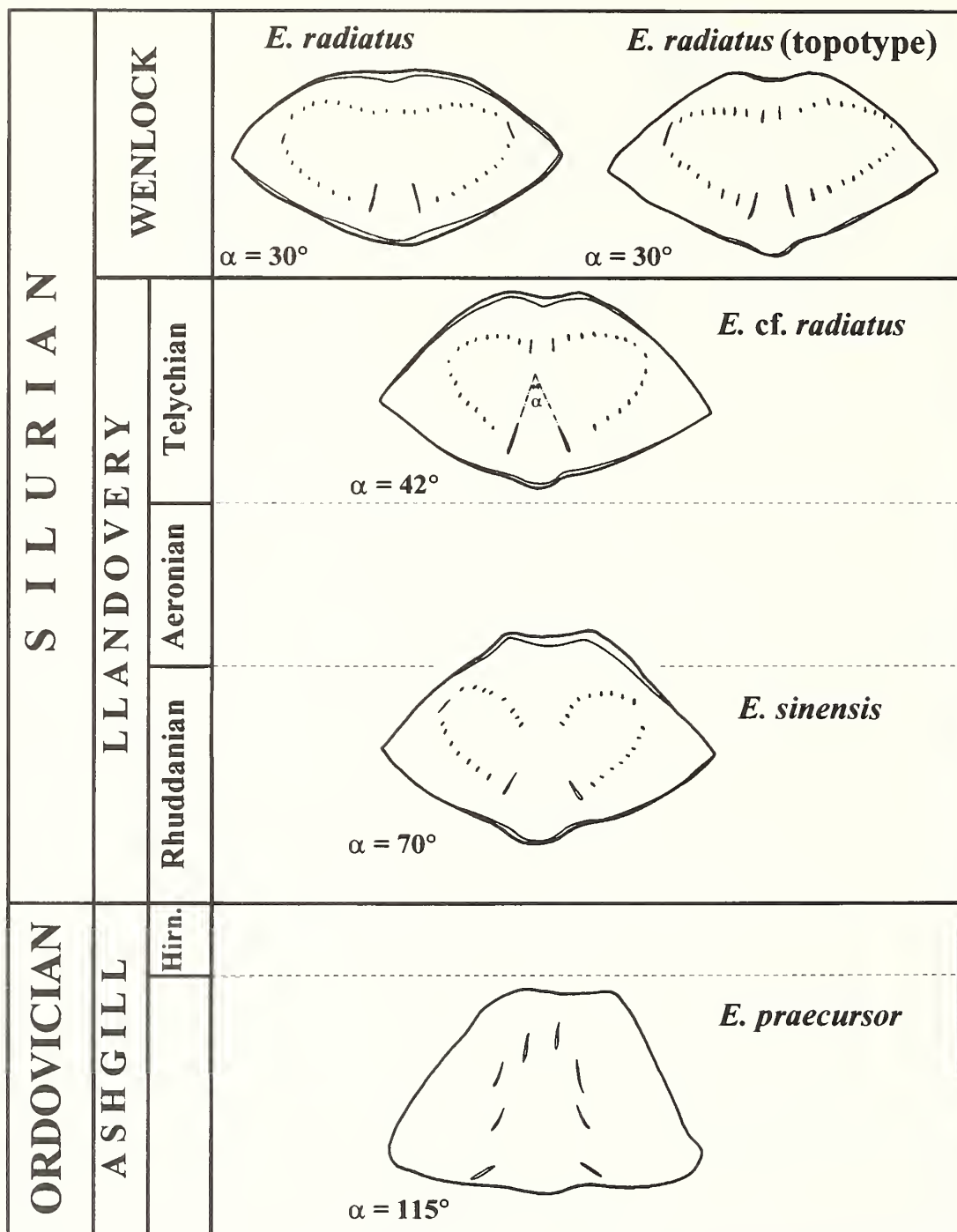


TEXT-FIG. 23. Reconstruction of one specimen of *Striispirifer yunnanensis* Rong and Yang, 1978; based on Text-figure 19.

TABLE 1. Measurements of the cross angle of a pair of jugal processes (α) at a given transverse section level in the following species based on the serial transverse sections examined in this paper. (S: smaller individual; L: larger individual). Note that no jugal processes have been found in *Eospirifer minutus* and *E. songkanensis*.

	(α)
1. <i>Eospirifer cinghizicus</i>	50°
2. <i>E. praecursor</i> (S)	70°
3. <i>E. praecursor</i> (L)	120°
4. <i>E. radiatus</i> (Sweden)	30°
5. <i>E. radiatus</i> (England)	35°
6. <i>E. cf. radiatus</i>	45°
7. <i>E. sinensis</i>	70°
8. <i>Striispirifer acuminiplicatus</i>	30°
9. <i>S. plicatellus</i>	80°
10. <i>S. yunnanensis</i>	20°

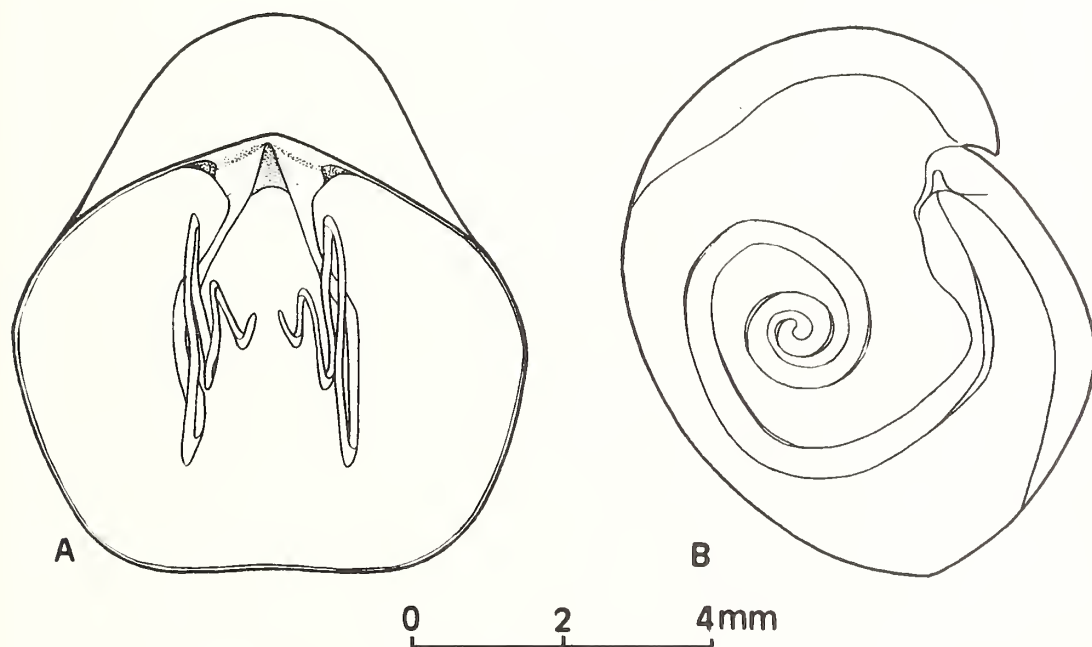
early Hirnantian (*Normalograptus extraordinarius* Biozone) but appeared in Tasmania in the late Hirnantian (*Glyptograptus? persculptus* Biozone) and in Asia (Kazakhstan and South China) and Australia (Tasmania) in the early-mid Rhuddanian (*Parakidograptus acuminatus* to *Cystograptus vesiculosus* biozones). *Eospirifer* did not become extinct at the end of the Ordovician; it had many advanced evolutionary novelties and evolved successively. It appears to have become adapted to shallow marine environmental conditions during the recovery interval (late Rhuddanian to early Aeronian) in some regions of Asia, including South China (Rong and Yang 1978, 1981), Tarim (Rong's identification for the materials of the Kalpintake Formation, provided by Zhang Shi-ben), Kazakhstan (Borisiak 1955; Olenicheva, pers. comm. 1992), and Ningxia, North China (Fu 1985). It did not arrive in Siberia, Avalonia, Baltica, southern Europe, North and South America, and other parts of the world until the late Aeronian (*Monograptus sedgwickii* Biozone) to early Telychian (*Spirograptus turriculatus* Biozone) when the eospiriferines diversified worldwide.



TEXT-FIG. 24. An inferred evolutionary trend in the angle between the jugal process at a given transverse section level in Ashgill, Llandovery and Wenlock species of *Eospirifer*. Hirn. = Hirnantian.

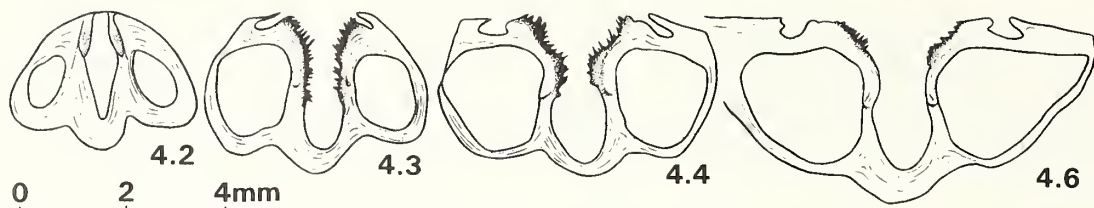
TABLE 2. Measurements of L_1/DL (distance between jugal process/length of dorsal valve), T_1/T (distance of ventral and dorsal valve at the level of jugal process/shell depth), T_2/T_1 (distance between ventral end of jugal process and dorsal valve floor/distance of ventral and dorsal valve at the level of jugal process), L_2/DL (distance between anterior end of spirillum and posterior end of dorsal valve/length of dorsal valve). *Eospirifer praecursor* (s) is a smaller specimen with a 3.1 mm wide shell; *E. praecursor* (l) one of the largest specimens collected with a 6.1 mm wide shell. (For abbreviations, see Text-figure 15).

Taxon	L_1/DL	T_1/T	T_2/T_1	L_2/DL
1. <i>Eospirifer minutus</i>	41.6	100	30.7	77
2. <i>E. praecursor</i> (s)	33.2	95.7	15.3	86.7
3. <i>E. praecursor</i> (l)	45	99.4	41.2	61
4. <i>E. radiatus</i> (England)	32.8	98.1	37.2	85.1
5. <i>E. radiatus</i> (Sweden)	39.8	99	35.6	84
6. <i>E. cf. radiatus</i>	32.7	99.5	34.9	82.9
7. <i>Striispirifer acuminiplicatus</i>	33	100	36	80
8. <i>S. plicatellus</i>	45	98	24	85
9. <i>S. yunnanensis</i>	33	100	26	80



TEXT-FIG. 25. Reconstruction of brachidia of *Cyclospira bisulcata* (Emmons, 1842) from the Hiller Member, Cobourg Formation (upper Caradoc), the type locality, 600 m east-north-east of Rodman, along Gulf Stream, New York (following text-figure 13 of Copper 1986).

This distribution suggests that the tectonic blocks, including South China, Tarim, Alxan, Australia and Kazakhstan, were palaeogeographically located relatively close to each other and could have undergone faunal exchanges by appropriate oceanic current systems. They were probably located more distantly from Siberia, Europe and America during the earlier Llandovery.



TEXT-FIG. 26. The striated cardinal process in four transverse sections of a topotype specimen of *Eospirifer radiatus* (Sowerby, 1834) (same specimen as used in Text-figure 12).

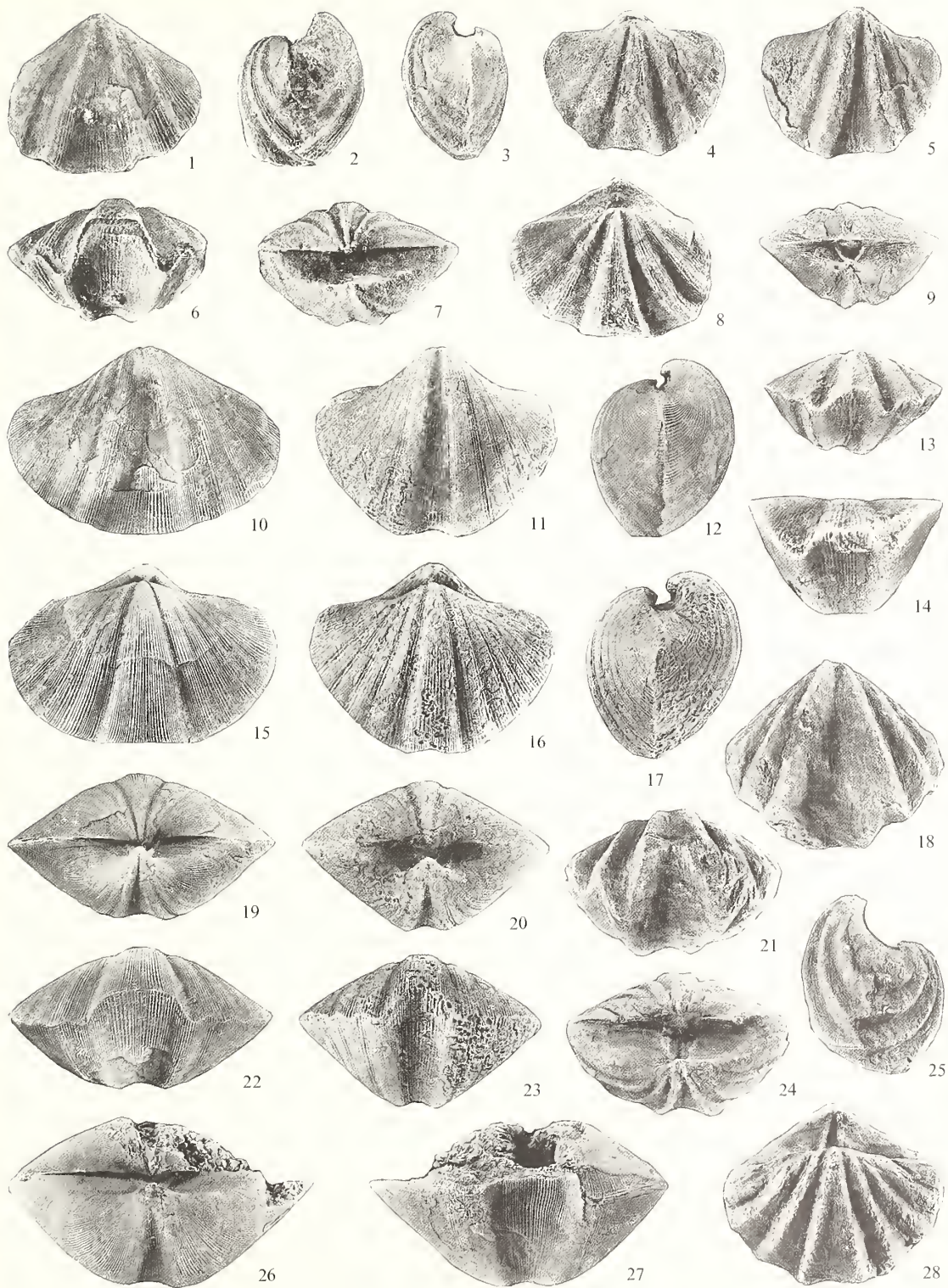
Suggested environmental model for the origin of the Spirifer Group

Jablonski and Bottjer (1990) proposed a pattern of environmental migration for the early history of major post-Palaeozoic clades (at ordinal level), where the first recorded members of the clades were usually confined to inshore sites, with an expansion subsequently across-shelf and in some cases, eventual restriction to deep water slope/basin sites. The *Spirifer* group (Order Spiriferida) is one of the most diverse groups of Brachiopoda in the Phanerozoic and it is worthwhile to test this model using spiriferid data. Accepting the eospiriferines as the most primitive spiriferides, *Eospirifer* as the most primitive eospiriferine, and *E. praecursor* as the earliest known *Eospirifer*, data are available to test Jablonski and Bottjer's model (1990).

All of the type material of *E. praecursor*, from the Changwu Formation (mid Ashgill), Pengli, Jiangshan County, south-western Zhejiang Province, East China, is preserved as internal and external moulds in a yellowish-green mudstone bed (Rong *et al.* 1994). Conjoined valves of this species have been collected from the contemporaneous Xiazhen Formation, Zhuzhai, Yushan County, north-eastern Jiangxi Province, about 32 km south-west of Pengli (see Text-fig. 1). Twenty-nine external and internal moulds of ventral or dorsal valves have been found at Pengli (Rong *et al.* 1994) and a huge number of the individual specimens (nearly 5000) at Zhuzhai. An assignment of *E. praecursor* at Pengli to Lower BA 3 to upper BA 4 was suggested by Rong *et al.* (1994, p. 771), but this is not the case for the occurrence at Zhuzhai. According to a new study of mid Ashgill brachiopod synecology in the Jiangshan–Yushan area, the *E. praecursor* Community has been proposed for an association consisting of the very abundant eponymous species, usually exceeding 99 per cent. of the whole biomass on the same bedding plane (Zhan and Rong 1995). The other

EXPLANATION OF PLATE 4

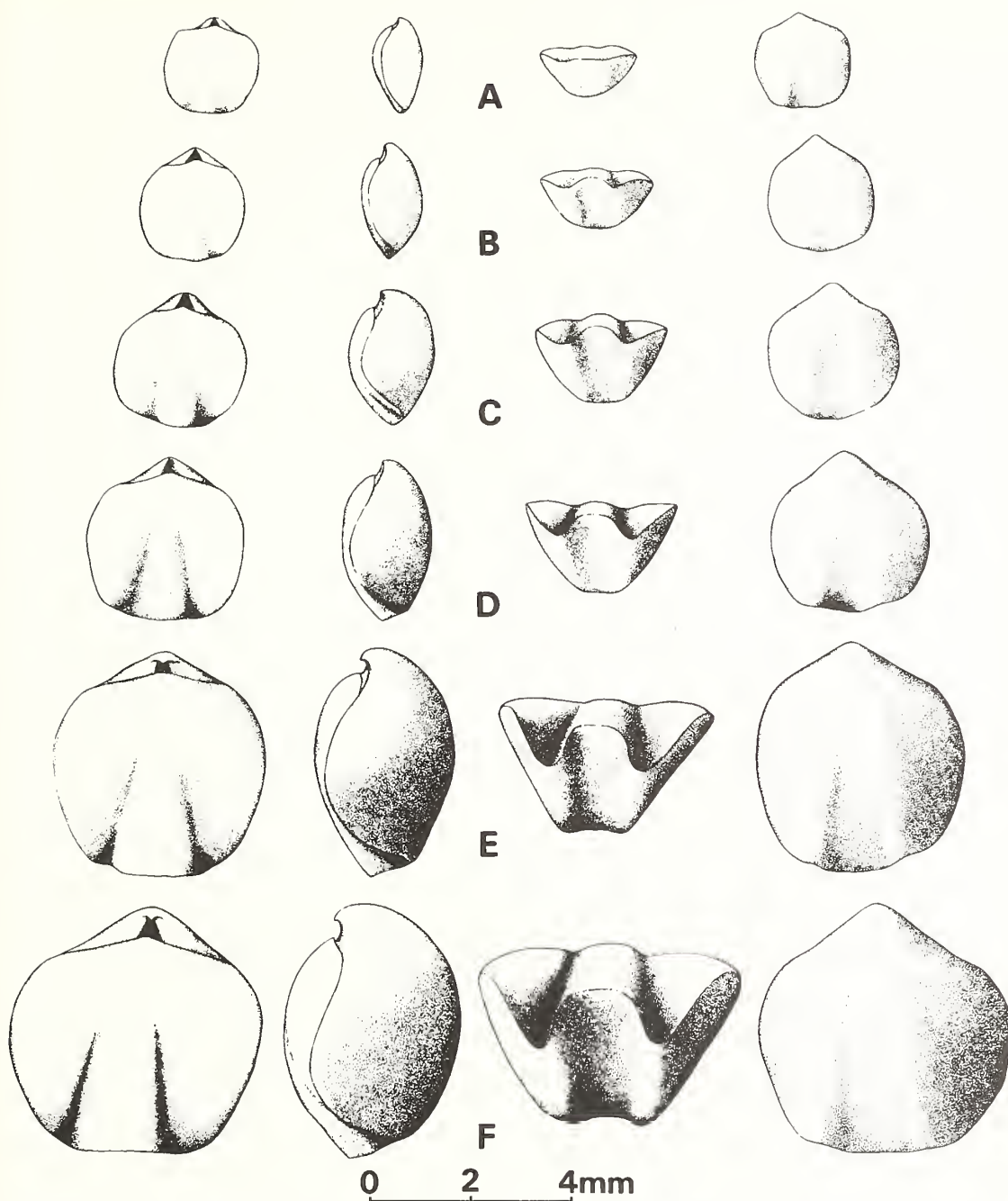
- Figs 1–2, 6–8, 18, 21, 24–25, 28. *Striispirifer acuminiplicatus* Rong, Xu and Yang, 1974; Lower Xiangshuyuan Formation (lower Aeronian, Middle Llandovery); Leijiatun, Shiqian, north-eastern Guizhou, South-west China. 1–2, 6–8, NIGP 22290, holotype; ventral, lateral, anterior, posterior and dorsal views of conjoined valves; $\times 3$. 18, 21, 24–25, 28, NIGP 44067, topotype; ventral, anterior, posterior, lateral and dorsal views of conjoined valves; $\times 2$.
- Figs 3–5, 9, 13. *Striispirifer yunnanensis* Rong and Yang, 1978; NIGP 124763, topotype; Kuantu Formation (Upper Ludlow); Qujing, eastern Yunnan, South-west China; lateral, dorsal, ventral, posterior and anterior views of conjoined valves; $\times 3$.
- Figs 10–12, 15–17, 19–20, 22–23. *Striispirifer plicatellus* (Linnaeus, 1758); Wenlock Limestone Formation (Homerian, Late Wenlock); Wenlock Edge, Shropshire, England. 10, 12, 15, 19, 22, NIGP 124764; ventral, lateral, dorsal, posterior and anterior views of conjoined valves; $\times 1.5$. 11, 16–17, 20, 23, NIGP 124765; ventral, dorsal, lateral, posterior and anterior views of conjoined valves, $\times 2$.
- Figs 26–27. *Eospirifer* cf. *radiatus*; NIGP 124758, the same specimen as Pl. 2, figs 10–11; posterior and anterior views of conjoined valves; $\times 1.5$.



members of the community are extremely rare; they include brachiopods (*Ovalospira* and *Antizygospira*), gastropods, bivalves, nautiloids, bryozoans and trilobites. They occur chiefly in calcareous mudstone and micritic limestone. Burrows can be seen in the mudstone. Sometimes, mud-cracks are well developed and a huge number of individuals of *E. praecursor* are present on the bedding plane of the micritic limestone. Rong and Zhan (1995) have suggested an assignment of this community to BA 2, indicating a near shore, very shallow water, normal marine environment with low energy. Although *E. praecursor* was adapted to relatively wide range of environments (through mostly very shallow water (BA 2 at Zhuzhai, most abundant), moderately deeper water (BA 3–4 at Pengli, uncommon), to occasionally deepest water in a low diversity *Foliomena* Fauna (BA 5 at Changwu, very rare)), disparity of numbers of *E. praecursor* in different associations indicates that this taxon may have preferred to inhabit a much shallower water habitat (BA 2) as at Zhuzhai than the relatively deeper water (BA 3–4) at Pengli. If this interpretation holds, it suggests that the Spiriferida originated in nearshore environments.

Conclusions

1. The late Ordovician *Eospirifer praecursor* Rong, Zhan and Han, 1994, is the earliest known eospiriferine and may be considered to be the ancestor of Silurian and Devonian eospiriferines.
2. New evidence confirms the possibility that the eospiriferines originated from a late Ordovician atrypoid stock possessing a simple spiralium directed centrally.
3. *Eospirifer*, a progenitor and Lazarus genus, originated in Asia (East China and ?Kazakhstan) during the mid Ashgill and then migrated into unknown areas (refugia) in the Hirnantian and survived the latest Ordovician mass extinction. It recovered and expanded its range into a number of regions (South China, Qaidam, Tarim, Kazakhstan, and Australia) in the Rhuddanian and early Aeronian, and migrated to Europe and America in the late Aeronian (about *sedgwickii* Biozone) to Telychian.
4. The late Rhuddanian *Striispirifer orbiplicatus* Fu, 1982 (p. 176, pl. 45, fig. 5) from southern Ningxia, north-eastern marginal belt of the Qaidam Plate, and the early Aeronian *Striispirifer acuminiplicatus* Rong, Xu and Yang, 1974 (p. 202, pl. 93, figs 17–19) from north-eastern Guizhou, South-west China, are the two earliest known species of *Striispirifer* (junior synonym *Hedeina*). They are internally very similar to *Eospirifer sinensis* Rong, Xu and Yang, 1974, from the upper Rhuddanian of north-eastern Guizhou, and may have originated from *E. sinensis* by development of rare plications on the flanks.
5. Presence of a striated cardinal process in *Eospirifer radiatus* (Sowerby, 1834), type species of the genus, from the type locality and horizon suggests that it cannot be considered to be an important and distinctive feature for tracing the genera in the eospiriferines.
6. Almost all large-scale evolutionary novelties in the eospiriferines were established at the outset of their history during the late Ordovician when *Eospirifer* originated, indicating that *Eospirifer* is a successive progenitor genus. The eospiriferines seem to have undergone later stabilization in the Silurian and Devonian. Development of crural plates, probably in the earliest Silurian, is a later macroevolutionary change or lag which is of significance in the evolution of the eospiriferines.
7. A probable shallower water environmental model is suggested for the origin of the order Spiriferida.



TEXT-FIG. 27. Variations of shell outline, convexity, ventral beak and sulcus in six specimens (A-F) of *Eospirifer praecursor* Rong, Zhan, and Han, 1994, from the Xiazhen Formation (middle Ashgill), Zhuzhai, Qunli, Yushan north-eastern Jiangxi, East China.

SYSTEMATIC PALAEONTOLOGY

Order SPIRIFERIDA Waagen, 1883

Superfamily CYRTIOIDEA Fredericks, 1924

Family EOSPIRIFERIDAE Schuchert and LeVene, 1929

(= HEDEINOPSIDAE Gourvennec, 1991)

Genus EOSPIRIFER Schuchert, 1913

Type species. Eospirifer praecursor Rong, Zhan and Han, 1994.*Eospirifer praecursor* Rong, Zhan and Han, 1994

Plate 1, figures 1–17; Plate 3, figures 7, 16; Text-figures 4–5, 27

1994 *Eospirifer praecursor* Rong, Zhan, and Han, p. 772, figs 9.1–18.*Type locality and horizon.* Changwu Formation (middle Ashgill), Pengli, Hejiashan, Jiangshan County, south-western Zhejiang Province, East China.*Materials.* Nearly 5000 conjoined valves.*Diagnosis.* See Rong *et al.* 1994, p. 772. Lacking crural plates.*Description.* The following is based on the conjoined valves.

Exterior. Very small shells, usually 4–5 mm long and wide, 3–3.3 mm deep, the largest known individual 6.5 mm long and wide, 4.5 mm thick; round pentagonal in outline; generally ventri-biconvex in lateral profile, rarely plano-convex or even gently concavo-convex. Ventral beak small, strongly curved; umbo swollen; interarea short, well-developed, slightly to strongly curved; delthyrium small with narrow delthyrial ridges almost perpendicular to the interarea; hinge line straight, about three-quarters or a little more of shell width; dorsal interarea extremely low. Ventral valve strongly convex, about three-quarters to four-fifths of the shell depth; ventral sulcus strongly developed, starting from the apex, shallow, wide, and flat at the base of sulcus, the widest part of the sulcus about half the shell width. Dorsal valve gently convex, sometimes flat or even occasionally slightly concave on the anterior part of the shells; fold prominent but flat, starting anterior to the umbo, lower than flanks, bounded by relatively deep and round furrows. Microsculpture of very fine costellae, generally 14–16 per mm in larger shells (usually 4.5–6 mm in shell width), occasionally 24–25 per mm in very small shells (less than 3 mm in shell width), increasing mainly by bifurcation; concentric lines very rare, if present, most irregular, in particular, near the anterior commissure.

Ventral interior. Teeth small, dental plates fine and short, about one-sixth of the valve length, slightly divergent ventrally.

Dorsal interior. Sockets small, cardinal process non-striate; no crural supporting plates; crura thick and stick-like posteriorly, then plate-like centrally and anteriorly, extending slightly divergently, located close to the dorsal valve, and being smoothly continuous with primary lamellae (= the first half whorl of each spiralium distal from its attachment to crus); a simple spiralium with only three to four whorls, occupying about 50 per cent. of the internal space of both valves in the adult growth stage and extending near the anterior margin; spiralia directed ventro-laterally with the primary lamellae separated, directed slightly divergent and near the sagittal plane; no jugum between two spirally coiled supports for lophophore (Text-figs 4–5).

Variation. Ontogenetic variation within a single population of *Eospirifer praecursor* from the Xiazhen Formation at Zhuzhai, Qunli, Yushan is marked. In addition to those features mentioned above, there are three other aspects as follows: (1) shell outline, generally rounded pentagonal in both smaller and larger specimens but having a slightly elongate circular outline in a small proportion of the individuals; (2) convexity of dorsal valve usually low, about one-quarter of ventral valve convexity, some larger specimens with slightly concave anterior part of dorsal valve, some dorsal valves entirely convex; (3) ventral beak and interarea, from almost erect to curved during its ontogeny: where shell size smaller than 3.5 mm, the beak is almost erect and the interarea

flat, apsacline; where the shell is larger than 3.5 mm, the beak is slightly curved and the interarea also curved, slightly anacline (Text-fig. 27).

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APPENDIX

In this paper serial sections and reconstructions of brachidia are shown for the following species assigned to *Eospirifer* and *Striispirifer* (including *Hedeina*), with the exception of *Eospirifer cinghizicus* and *E. songkanensis*.

Eospirifer

1. *E. cinghizicus* Borisiak, 1955: *cinghizicus* Bed of Al'peisskii Horizon (Llandovery), Chinghiz, Kazakhstan (provided by Dr M. A. Olenicheva; see also Borisiak 1955, p. 68, pl. 12, figs 6–9; and this paper).
2. *E. minutus* Rong and Yang, 1981: the lower–middle Xiangshuyuan Formation (lower Aeronian, Middle Llandovery); Yingwuxi, Sinan County, north-eastern Guizhou Province, South-west China (see also Rong and Yang 1981, p. 372, pl. 1, figs 17–20).
3. *E. praecursor* Rong, Zhan, and Han, 1994: Xiazhen Formation (middle Ashgill), Zhuzhai, Yushan County, north-eastern Jiangxi Province, East China (this paper). The type horizon and locality of this species are upper part of Changwu Formation (middle Ashgill); Pengli, south-west part of Jiangshan County, western Zhejiang Province, East China (see also Rong *et al.* 1994, p. 772, figs 7, 8.2, 9.1–9.18, 10).
4. *E. radiatus* (Sowerby, 1834): topotype, Much Wenlock Limestone Formation (uppermost part of Wenlock, *ludensis* Biozone), Dudley, West Midlands, England (provided by Dr L. R. M. Cocks) (see also St Joseph 1935, p. 322, text-fig. 3 and this paper).
5. *E. radiatus* (Sowerby, 1834): Mulde Beds (SW16) (middle–upper Wenlock), Gotland, Sweden (provided by Dr P. Copper); (see also Boucot 1963, p. 685, pl. 97, figs 1–6; Cocks 1978, p. 161; and this paper).
6. *E. cf. radiatus*: Jupiter Formation (C650) (Telychian, Upper Llandovery); Firetower Road, north of Firetower, Anticosti, Canada (provided by Dr P. Copper; this paper). This species is characterized by a complete deltidium covering the whole delthyrium and without any kind of plications at the shell marginal area which can be distinguished from *E. radiatus* (Sowerby) of England.
7. *E. sinensis* Rong, Xu and Yang, 1974: the base of Xiangshuyuan Formation (upper Rhuddanian, Lower Llandovery); Leijiatun, Shiqian County, north-eastern Guizhou Province, South-west China (see also Rong *et al.* 1974, p. 201, pl. 93, figs 34–36; Rong and Yang 1978, p. 371, pl. 1, figs 1–3, 11, 16, 21–26, 29, 33, 34; and this paper).
8. *E. songkanensis* Wu *in* Rong and Yang, 1978: upper part of the Shihniulan Formation (upper Aeronian, Middle Llandovery); Hanjiadian, Songkan, Tongzi, northern Guizhou Province, South-west China (provided by Dr Wu Hao-ruo; see also Rong and Yang 1978, p. 373, pl. 1, figs 27–28, 31–32; and this paper).

Striispirifer

1. *S. acuminiplicatus* Rong, Xu and Yang, 1974: Lower Xiangshuyuan Formation (lower Aeronian, Middle Llandovery); Leijiatun, Shiqian, north-eastern Guizhou Province, South-west China (see also Rong *et al.* 1974, p. 202, pl. 93, figs 17–19; Rong and Yang 1978, p. 375, pl. 1, figs 4–6, 12–15, 30; and this paper).
2. *S. plicatellus* (Linnaeus, 1785): Much Wenlock Limestone Formation (Homerian, Upper Wenlock); Wenlock Edge, Shropshire, England (provided by Dr L. R. M. Cocks; see also Boucot 1963, p. 696, pl. 100, figs 8, 14–15; Cocks 1978, p. 163; and this paper).
3. *S. yunnanensis* Rong and Yang, 1978: Kuantu Formation (Upper Ludlow); Xiaoxiang Reservoir, south-west of Qujing, eastern Yunnan Province, South-west China (see also Rong and Yang 1978, p. 377, pl. 3, figs 26–27, 30; and this paper).

EARLY ORDOVICIAN (ARENIG) BIVALVES FROM THE LLANGYNOG INLIER, SOUTH WALES

by JOHN C. W. COPE

ABSTRACT. The most diverse early Ordovician bivalve fauna yet known comprises 20 species belonging to 18 genera. It is from the early Arenig (Moridunian Stage) of the Llangynog Inlier, near Carmarthen, South Wales, and is dominated by actinodontoids, with palaeotaxodonts, cyrtodontoids and rarer modiomorphoids, anomalodesmatans, solemyoids and a pteriid. From the same locality a rostroconch is described and a nearby mid-Arenig (Whitlandian Stage) locality has yielded an ambonychiid. The following new taxa are described: *Pensarnia laeviformis* gen. et sp. nov., *Paulinea parva* gen. et sp. nov., *Ovatoconcha fragilis* gen. et sp. nov., *Glyptarca serrata* sp. nov., *Carminodonta crossi* gen. et sp. nov., *Fortowensia grandis* gen. et sp. nov., *Celtoconcha foveata* gen. et sp. nov., *Moridunia simplicidens* gen. et sp. nov., *Goniophora* (*Cosmogoniophorina*) *extensa* sp. nov., *Parallelodus dyfedensis* sp. nov., *Falcatodonta costata* gen. et sp. nov. and *Arenigomya carinata* gen. et sp. nov. The new genus *Hemiprionodonta* is introduced for forms previously described from the middle Ordovician of France and Iberia, and from the upper Ordovician of North Wales. The following higher level taxa are proposed: Superfamily Glyptarcoidea, Family Glyptarcidae, Order Cyrtodontida, Superfamily Falcatodontoidea and Family Falcatodontidae. The fauna includes the earliest known representatives of the solemyoids, pterioids and anomalodesmatans.

VERY few bivalves are known from rocks of pre-Arenig age. The earliest unequivocal records are from rocks of early Cambrian age. *Pojetaia* Jell, 1980 is undoubtedly an early palaeotaxodont bivalve; *Fordilla* Barrande, 1881 is of less certain affinities, and whilst it is regarded by most authorities as a bivalve (see Runnegar and Bentley 1983) not all agree with the views of Pojeta and Runnegar (1985) that it is a precursor of the modiolopsid bivalves of the Ordovician. Subsequently this view has been modified since the shell structure of these two genera has been shown to be remarkably similar (Runnegar and Pojeta 1992). Earlier than either of these is *Yangtzedonta* Yu, 1985 from the Meishucunian Stage of the Lower Cambrian; unfortunately this is known from only one valve, which has no muscle scars, and its bivalve affinities are thus uncertain. *Yangtzedonta* is just one example of a whole series of putative early Cambrian bivalves recorded in the literature; many of these were reviewed by Runnegar and Pojeta (1992) and all were assigned to other groups. Later Cambrian bivalves than these are unknown, and all recorded genera have been shown subsequently to belong to other phyla or molluscan classes (see Runnegar and Pojeta 1992). This was, for example, the fate of *Lamellodonta*, at the time of publication of the bivalve volume of the *Treatise on invertebrate paleontology* (Cox *et al.* 1969) the earliest supposed bivalve, later shown to be a distorted obolid brachiopod (Havlíček and Kříž 1978).

It is not until the early Ordovician that bivalves re-appear in the fossil record. From the Tremadoc Series, three records may be accepted unequivocally: those of Harrington (1938) from Satta Province, Argentina, of Pojeta and Gilbert-Tomlinson (1977) from the Amadeus Basin of Australia, initially recorded as of Arenig age, but subsequently shown to be of latest Tremadoc age (Shergold *et al.* 1991), and of Babin (1982) from the Montagne Noire. The record of a Tremadoc form from Afghanistan (Desparmet *et al.* 1971) is of uncertain early Ordovician age (Babin and Gutiérrez-Marco 1991). The nine or ten Tremadoc species include palaeotaxodonts, palaeo-heterodonts and cyrtodonts. Thus Tremadoc bivalve faunas are exceptionally rare and of low diversity. From the lower part of the succeeding Arenig Series, bivalves have hitherto been described from four areas:

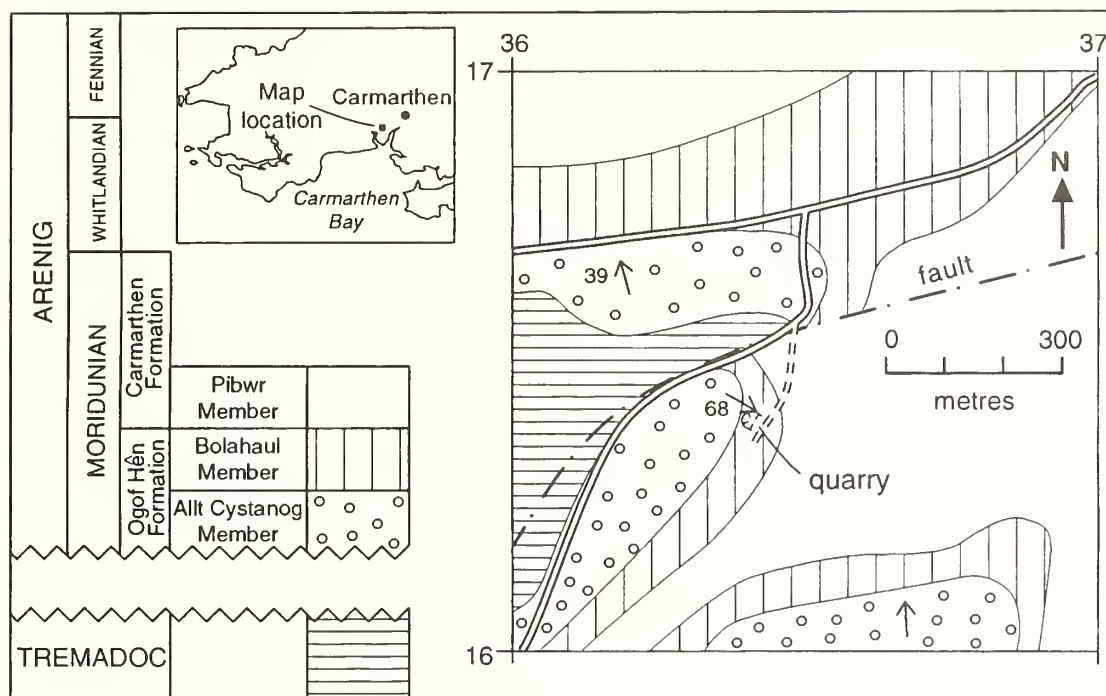
1. Ramsey Island, South Wales (Hicks 1873). The fauna, initially ascribed a Tremadoc age, was redescribed by Carter (1971) who reduced Hick's faunal list to five species. The specimens are very poorly preserved, and remain largely uninterpretable.
2. The Montagne Noire, southern France (Thoral 1935; Babin 1982). This fauna is generally well preserved and the Lower Arenig part contains seven species.
3. Salta Province, northern Argentina (Harrington 1938). An indifferently preserved fauna comprises three species.
4. The Moroccan Anti-Atlas (Babin and Destombes 1992). The early Arenig part of the fauna includes two specifically identifiable forms, both also known from the Montagne Noire.

Higher in the Arenig Series bivalves become more common, and have been reported from, in addition to localities 2. and 4. above, the Massif Armoricaire, northern France (Barrois 1891; Babin 1966 – upper Arenig), Sweden (Soot-Ryen 1969 – upper Arenig), and Argentina (Sanchez and Babin 1993 – upper Arenig). The other early Ordovician bivalve occurrences listed by Pojeta (1971) (e.g. Billings 1865; Sardeson 1896; Butts 1941; Cloud and Barnes 1948) have proved either to be records of rostroconchs, or are not now considered to be early Ordovician. Because of this exceptional rarity, the discovery of a well preserved and diverse fauna from rocks of early Arenig (Moridunian Stage) age, consisting of 20 species, belonging to 18 genera, is clearly of considerable importance.

The fauna occurs in a small quarry (Text-fig. 1) in the northern part of the Llangynog Inlier (Cope 1982), an area of rocks of Precambrian to Arenig age (Cope 1980), and is some 6 km to the south-west of Carmarthen, Dyfed, South Wales (Grid reference SN 3640 1639). The quarry was first mentioned by the Geological Survey (Strahan *et al.* 1909, p. 16) whose meagre faunal list reads '*Dictyonema?*, *Lingula* cf. *attenuata* J. de C. Sowerby, *Orthis calligramma* Dalman, *Orthis* sp., and a lamellibranch'. Here are exposed interbedded siltstones and mudstones of the early Arenig (Moridunian Stage) Bolahaul Member of the Ogof Hên Formation (Fortey and Owens 1978) which can be seen to overlies directly conglomerates of the Allt Cystanog Member of the same formation, and thin stringers of conglomerate and occasional pebbles are features of the sedimentary rocks in the quarry. Bioturbation is common and the rock is an intimate admixture of silt and clay fractions. The fauna is well dated by the trilobites *Merlinia murchisoniae* (Murchison) and *Neseuretus ramseyensis* Hicks, shown by Fortey and Owens (1987) to be characteristic of the Moridunian Stage. The unequivocal evidence of age of these rocks is important, for not only have they yielded the earliest known bryozoan (Taylor and Cope 1987) and parablattoid (Paul and Cope 1982), but representatives of the bivalve fauna include the earliest members of their family, order, or in some cases, subclass. Further new forms belonging to other classes of molluscs and to other phyla remain to be described; many of them too are the earliest representatives of their groups. The quarry has been scheduled as a Site of Special Scientific Interest (SSSI) under the protection of the Countryside Council for Wales (CCW). Anyone wishing to visit the locality, which is on private property, must first obtain permission from the CCW.

The reason for the preservation of this exceptionally diverse fauna may be briefly examined. Its extremely local nature is noteworthy; similar horizons, over a wide area around Carmarthen, have faunas dominated by brachiopods and contain few, if any bivalves. I have concluded that the exceptional diversity represented by the fauna in this one quarry is because it is from a close inshore environment, such as is not often preserved in the geological record. This habitat seems to have been the place where major evolutionary change was occurring, presumably in response to increased competition there. If it is indeed the case that the inshore environment was the source of much evolutionary pressure, it is not surprising that evolutionary intermediates are often lacking in the fossil record: they are to be found most often in the rarely preserved near-shore deposits, which, once identified, seem to have not only exceptionally diverse faunas, but to contain a significant number of first appearances of taxa at levels from specific up to class level.

Studies of the evolution of Phanerozoic marine communities by Sepkoski (1981) and Sepkoski and Miller (1985) have suggested that mollusc-dominated faunas are characteristic of the Mesozoic and Cenozoic. These 'modern faunas' displaced the brachiopod-dominated 'Palaeozoic faunas'



TEXT-FIG 1. Location of the source of the Arenig bivalve fauna in the Llangynog Inlier, its geological context and stratigraphical position.

progressively, from the Ordovician onwards, particularly in the near-shore environment. It is not until after the late Permian extinctions, however, that the 'modern faunas' are dominant. The Llangynog fauna is clearly the earliest mollusc-dominated fauna yet recorded (71.5 per cent. of the fauna), and for this reason alone is of considerable interest.

Although the fauna is exceptionally diverse, many horizons in the quarry proved virtually unfossiliferous, whereas others occasionally yielded abundant fossils belonging to many taxa. Altogether, almost 20 tonnes of rock were collected and split in the laboratory and have yielded a total of over 3100 fossils. Predominant amongst the fossils are bivalves (40.7 per cent.); also occurring are nautiloids (25.6 per cent.), brachiopods (17.9 per cent.), gastropods (4.5 per cent.), dendroids (3.9 per cent.), trilobites (2.4 per cent.), conulariids (1.6 per cent.), hyolithids (1.0 per cent.), monoplacophorans (0.7 per cent.), and parablattoids (0.6 per cent.). The remaining 1.1 per cent. consists of (in approximate descending order of abundance): a problematical coral-like organism, receptaculitids, gorgoniids, sponges, ostracods, eocrinoids, bryozoans and single specimens of graptoloid, rostroconch, crinoid and calcified red alga. In addition to being the most abundant, the bivalves are also the most diverse group in the fauna. In view of ideas about the completeness of the fossil record (e.g. Paul 1985) it is noteworthy that in this collection about ten taxa are each represented only by a single specimen.

The bivalve fauna is largely preserved as limonite-covered moulds; material from the more argillaceous horizons generally lacks the limonite coating and the moulds are pale grey in colour. Both form excellent material for investigation of the morphology of the shell. Dentition is commonly perfectly preserved and external moulds allow full appraisal of the external ornament. Unusually for deposits of this age, some bivalve taxa are represented by hundreds of specimens, thus allowing a study of intraspecific variability to be carried out on material which has not been

significantly distorted. After hardening of the moulds with polyvinyl acetate, latex casts may be readily made which allow the full morphology of the shell to be reconstructed. A few bivalves have silicified shells; a few others are preserved as composite moulds (McAlester 1962), and most rarely some specimens have not been completely decalcified.

The most obvious character of the bivalve fauna is that the vast majority of the material is very small, although little material appears to represent juvenile specimens. Only one or two species exceed 25 mm in length and much of the material is around 10 mm long. Disarticulated valves predominate, although a significant number of conjoined valves have been found for most species. From this one can conclude that the fauna represents a death assemblage. Although the specimens are disarticulated, they are, however, mostly devoid of signs of wear, suggesting that there has been no significant transport. This is emphasized by preservation of the most delicate structures on some of the fossils, such as the brachioles of the parablastoids (Paul and Cope 1982). Some species of bivalve are represented predominantly by conjoined valves, and it is probable that these were more deeply infaunal, with the specimens possibly representing an *in situ* death assemblage. In some cases the two disarticulated valves of the same specimen may be found in close proximity on the same bedding plane. It is clear that for the most part current activity was minimal and post-mortem drift, at least of the benthos, insignificant. Two occasional features do, however, indicate some degree of transport: in some cases two or three of the same valves of specimens of the same species have become stacked one within the other; in other cases the most prominent parts of the exterior of the shell appear to have suffered sufficient abrasion for growth increments to disappear.

SYSTEMATIC PALAEOLOGY

There are two classifications of bivalves which have more current use by palaeontologists than others; those of Cox *et al.* (1969) and of Pojeta (1987, which incorporates the latest modifications of his earlier (1978) classification). The two classifications differ significantly at subclass level. Since the publication of the *Treatise* much work has been published on Ordovician bivalves and the rostroconchs have been recognized as a separate class of molluscs. Pojeta has abandoned the subclass Cryptodonta because it contained a medley of taxa now properly assigned to other subclasses of bivalves and the class Rostroconchia; the order Solemyoida (*ex* Cryptodonta) is placed by Pojeta in the subclass Palaeotaxodonta. The modiomorphoids (*ex* Palaeoheterodonta) and mytiloids (*ex* Pteriomorphia) form the subclass Isofilibranchia Iredale, 1939; the Palaeoheterodonta and Heterodonta are combined in the subclass Heteroconchia Hertwig, 1895. As a result of conclusions drawn herein and by Cope (1995), it appears that the *Treatise* classification is closer to a true phylogenetic scheme, and the higher taxonomic subdivisions used are based on modifications to this.

Measurements are in millimetres, and were obtained using vernier calipers or a binocular microscope with eyepiece graticule. Length is the maximum length of the shell measured, as far as is possible to determine, parallel to the hinge-line; height is the maximum height of the shell measured at right angles to the length. For some of the palaeotaxodont bivalves the term hinge angle is used; this is the angle between the anterior and posterior parts of the hinge plate. For size description I describe as 'small' those specimens less than 10 mm long; 'medium-sized', lengths between 10 and 20 mm, and 'large' with length in excess of 20 mm.

Since a total of 1269 identifiable bivalves was collected, valid conclusions may be drawn concerning the relative abundance of the main groups. Since all evidence suggests that palaeotaxodonts were the earliest bivalves, it is perhaps surprising that they constitute only 12 per cent. of the fauna. In contrast, the palaeoheterodonts make up 78.3 per cent.: of these the dominant group is the actinodontoids (76.9 per cent.), whilst the modiomorphoids account only for some 1.4 per cent. Of the remaining groups, pteriomorphians account for 7.6 per cent., anomalodesmatans 1.7 per cent. and lipodontids 0.4 per cent. It is thus clear that if views on the history of the evolution of the filibranch gill are correct (Cope 1995), the evolutionary advantage of this gill as a feeding

organ seems to have become immediately apparent after its origin in the earliest Ordovician, for not only are the non-palaeotaxodont groups abundant, they are also very diverse.

All the material from the Llangynog localities has been deposited in the collections of the Department of Geology, National Museum of Wales, Cardiff. The bivalves described herein are registered under accession number NMW 78. 17G. The prefix BGS refers to material in the British Geological Survey, Keyworth. Unless specifically mentioned, all material is from the Moridunian Stage of the Arenig Series and from the quarry described above. Under the heading '*Material*' the following abbreviations are used: LV, left valve(s); RV, right valve(s); CV, conjoined valve(s). The suffix E with any of these indicates an external mould only.

Class BIVALVIA Linnaeus, 1758
Subclass PALAEOTAXODONTA Korobkov, 1954
Order NUCULOIDA Dall, 1889
Superfamily NUCULOIDEA Gray, 1824
Family PRAENUCULIDAE Pfab, 1934

Remarks. The number and relationships of genera within the family is still in a state of flux. The *Treatise* lists five genera which occur in the Ordovician. To these can be added *Concavodonta* Babin and Melou, 1972; *Fidera* Pojeta and Gilbert-Tomlinson, 1977 and *Eritropis* Pojeta and Gilbert-Tomlinson, 1977. None of the existing genera can accommodate the species described here and thus new ones are proposed.

Genus PENSARNIA gen. nov.

Derivation of name. From Pensarn, south of Carmarthen.

Type species. *Pensarnia laeviformis* sp. nov.

Diagnosis. Praenuculid of rounded trapezoidal outline with strongly inflated valves of variable length and prominent umbones at anterior. Posterior part of dorsal margin and anterior ventral margin approximately parallel. Exterior with fine growth increments, occasional stronger increments in some. Taxodont dentition continuous beneath umbones; anteriormost teeth largest; those beneath umbones extremely small; posterior teeth largely equal in size posterior to umbones; 20–32 straight or chevron-shaped teeth. Hinge-line straight as far as posterior, where it follows curve of dorsal margin of valves. Anterior adductor circular, deeply inserted and with prominent triangular pedal retractor scar on dorsal side; posterior adductor larger, more shallowly inserted, sub-trapezoidal. Umbones strongly curved over hinge-plate.

Stratigraphical range. Early–?mid Arenig, Moridunian–?Whitlandian stages.

Remarks. *Pensarnia* is similar to *Praenucula* Pfab, from the middle Ordovician of Bohemia, but differs in its orientation. Following the criteria of Bradshaw (1970), Bradshaw and Bradshaw (1971) and Tunnicliff (1982), it is clear that the umbones of *Praenucula* lie within the posterior half of the shell, whilst in *Pensarnia* they lie very much to the anterior. There are also differences in dentition. In *Praenucula* there is a gradational increase in the size of the teeth to the anterior and posterior of the umbones, and the subumbonal teeth are not markedly smaller. The anteriormost teeth of *Pensarnia* are also larger than in most species of *Praenucula*, and it may have been this latter feature which persuaded Morris (1978) to include this species in *Cardiolaria*, as *C. laevis*. However, in *Cardiolaria* the anterior teeth are larger still, and, more significantly, the anterior and posterior teeth belong to separate sets which overlap in the subumbonal region of the hinge plate. This latter feature was well illustrated by Babin and Gutiérrez-Marco (1991) and Bradshaw (1970). Nevertheless, the larger size of the anteriormost teeth of *Pensarnia* shows a superficial resemblance to *Cardiolaria*. The posterior adductor scar of *Praenucula* is of similar size to the anterior; both are

circular and both have rounded pedal muscle scars associated with them. These features contrast with those of *Paulinea* gen. nov. (see below, p. 985) which has unequal-sized adductor muscle scars, a triangular anterior pedal scar and a scarcely impressed (and thus seldom visible) posterior pedal scar. *Paulinea* also has a more rounded ventral margin.

Pensarnia laevisformis sp. nov.

Plate 1, figures 1–10

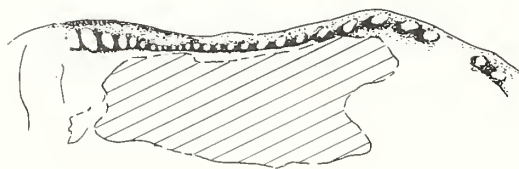
- non 1824 *Nucula laevis* Say, p. 141, pl. 10, fig. 5.
 1839 *Nucula? laevis* J. de C. Sowerby in Murchison, p. 635, pl. 22, fig. 1.
 1902 *Nucula laevis* J. de C. Sowerby; Blake, p. 9.
 1978 *Cardiolaria laevis* (J. de C. Sowerby); Morris p. 260, fig. 25.

Material. 59 specimens (32 LV, 23 RV, 4CV). Holotype: NMW 78. 17G. 1022. Paratypes: NMW 78. 1023–1077; Sowerby's material of *N.? laevis*, BGS Geological Society Collection 6849, three left valves from Pensarn, Carmarthen.

Diagnosis. As for genus (see above).

Derivation of name. Pro Sowerby's name *laevis* which is unavailable.

Description. All the material is of small size; the holotype is 9.0 mm long and 7.2 mm high. The anterior adductor is circular on the holotype, but other material shows that it can be subtriangular. It is deeply inserted and arising from its dorsal margin is a long triangular scar extending to the umbonal regions; in some specimens this scar is divided down its mid-line. The posterior adductor is not so deeply impressed and is subtrapezoidal rather than circular; a few specimens show a faint trace of posterior pedal muscle scar running dorsally from the posterior adductor.



TEXT-FIG. 2. *Pensarnia laevisformis*; NMW 78. 17G. 1063; camera lucida drawing of hinge region of left valve, internal mould; shaded area is matrix exposed by removal of umbo; $\times 10$.

The holotype is a right valve internal mould which shows five teeth anterior to and 15 posterior to the umbo, where the hinge-plate is damaged; other material shows up to ten anterior and 22 posterior teeth. In specimens where the umbo has been removed (e.g. Pl. 1, fig. 9) the teeth continue beneath the umbones, where, however, they become much smaller; it is not possible to see these teeth with the umbo in place as the hinge-plate lies so closely beneath the umbones. Up to ten teeth may be hidden from view in this way. The hinge-line is essentially straight and the hinge-angle is close to 180° on the holotype and on the majority of specimens. In forms where the hinge-line appears essentially straight, curvature is confined to its posterior extremity, where it follows the curve of the dorsal margin of the valves.

There is considerable variation in shape. Some examples are strongly truncated posteriorly, so that the hinge-line curves strongly at a point very much closer to the umbonal region than is normal for this species. Because these are so distinct it was thought they belonged to a separate species, but enough material was collected to establish that this is simply a posteriorly very abbreviated form, with intermediates occurring between it and the more usual morphologies. With this shortened hinge, the species appears to have a high hinge angle; this is the result of transposing the normal angle of the posterior part of the hinge-line closer to the umbo. In these posteriorly truncated forms (e.g. Pl. 1, figs 5–6) the posterior part of the hinge-line bends through an angle approaching 50° . Others are intermediate in shape (e.g. Pl. 1, fig. 7). Notwithstanding these differences in length, the posterior part of the dorsal margin remains closely parallel to the anterior part of the ventral margin. The teeth in any specimen may be straight or chevron-shaped.

The exterior of the shell is basically smooth, but some specimens show fairly regular, stronger growth increments, giving a coarse concentric ornament.

Remarks. *Nucula? laevis* (Sowerby in Murchison, 1839) is a junior homonym of *N. laevis* Say, 1824, from the Miocene of Chesapeake Bay, Maryland, and remained unused until its quotation by Morris (1978). Sowerby's material is a mudstone block with three palaeotaxodonts (BGS, Geol. Soc. Coll. 6849) which was identified as 'the type' by Blake (1902). No holotype was designated by Sowerby, who described the species as being three-and-a-half lines long and nearly two lines high (a line is equivalent to 2.1 mm). Dimensions of the largest specimen (Pl. 1, fig. 8) are 7.2 mm long and 4.0 mm high, a close correspondence with Sowerby's measurements; this is identified as the one that he described and is here designated the lectotype of his (unavailable) species. The label is badly faded, but the specimen is stated by Sowerby (*in* Murchison 1839, p. 635) to be from 'Pensarn, near Caermarthen in black schist' and the lithology is consistent with that exposed in the Roman Road section there, described in *The Silurian System*. The locality was re-collected by Fortey and Owens (1978) who assigned it to the Bolahaul Member of the Ogof Hên Formation, of the same age as the Llangynog fauna.

Sowerby's species was not referred to by Carter (1971) in his revision of the Ramsey Island fauna. *Ctenodonta menapiensis* Hicks, refigured by Carter (1971, pl. 38, figs 1–2) as *Praemucula menapiensis*, was described as being anteriorly elongated, with the umbones at the posterior; if it is a *Praemucula*, this orientation is correct, but it is possible that it was wrongly oriented by Carter. In that case, the pronounced anterior adductor impression could suggest that it belongs instead to *Pensarnia*. In view of the similar age and relative proximity of Ramsey Island, the two may well be congeneric, but as Hicks' material is so poorly preserved and considerably distorted, specific comparisons are meaningless.

Mr S. P. Tunnickliff has drawn to my attention specimens of *Pensarnia* from the Mytton Flags of Shropshire in the British Geological Survey collections. These clearly belong to the genus, but may represent a new species. They are of early or mid-Arenig age.

Genus PAULINEA gen. nov.

Derivation of name. For my wife, Pauline.

Type species. *Paulinea parva* sp. nov.

Diagnosis. Moderately inflated praenuculids with shape ventral to hinge semicircular to subcircular and prominent, generally blunt umbones within anterior half of shell, not strongly curved over hinge-plate. Hinge-line with graded series of peg-like taxodont teeth smaller beneath umbones and increasing in size outwards (gradidentate); hinge plate curved ventrally anteriorly and posteriorly. Anterior adductor circular, rather shallowly inserted, with dorsally situated pedal retractor scar visible in some; posterior adductor very shallowly inserted, larger, subcircular, often not discernible. Exterior of shell smooth or with occasional strong growth increments. Ventral margin of shell very thin.

Stratigraphical range. Early Arenig, Moridunian Stage.

Remarks. This genus is more rounded in outline than *Pensarnia*, has more gradually graded tooth size (gradidentate of Cope 1995) and the umbones are less pronounced on internal moulds and are not so strongly curved over the hinge-plate as in *Pensarnia*. The adductor muscles are also less deeply inserted than in the latter. *Paulinea* does not compare easily with any other praenuculid, and is readily distinguished by its shape, outline, and hinge-line.

Paulinea parva sp. nov.

Plate 1, figures 11–22

Derivation of name. From the Latin *parva* (= small), alluding to the small size of this species.

Material. 96 specimens (49 LV, 46 RV, 1 CV). Holotype: NMW 78. 17G. 1078. Paratypes: NMW 78. 17G. 1079–1173.

Diagnosis. As for genus.

Description. Moderately inflated praenuculid varying in shape from ovoid to subcircular, with well-defined umbo. The holotype, a right valve internal mould, is 6.5 mm long and 4.8 mm high and lies towards the larger end of the size range. Many of the paratypes are between 5.0 and 6.5 mm long, but some are even smaller. Morphologies vary from elongated forms (length: height ratio approaches 1.5:1; e.g. Pl. 1, fig. 11) through to those in which the ratio approaches 1:1 (Pl. 1, fig. 12). Thus NMW 78. 17G. 1110 is 7.7 mm long and 5.2 mm high and NMW 78. 17G. 1081 (Pl. 1, fig. 19) is 4.3 mm long and 4.2 mm high. The holotype shows a lightly impressed circular anterior adductor muscle scar, dorsal to which is a faint triangular impression of the anterior pedal retractor. The posterior adductor scar is quite faintly impressed and is subcircular; its area is about twice that of the anterior scar. A very faint area extending dorso-anteriorly from this scar may be a posterior pedal retractor. In many specimens the posterior adductor scar is not visible, but in the occasional specimen it may be pronounced.

The greatest length is achieved about half-way between the hinge-line and the ventral margin; both anterior and posterior margins are rounded. The hinge-line is generally significantly shorter than the shell length and a series of peg-like taxodont teeth are present. On the holotype there are five anterior to the umbo and seven behind; subumbonal teeth are not visible on the holotype, but other specimens show that teeth are continuous beneath the umbo, where they are smaller. The teeth may number up to 20; they follow the curve of the hinge-line anteriorly and posteriorly. The hinge-angle is close to 180°, but because the ends of the hinge-plate curve ventrally in many specimens the impression gained is of a smaller hinge angle.

The exterior of the shell is generally smooth, but a few forms have accentuated growth increments and in a further few these are so pronounced that the shell appears to have a pronounced commarginal ornament.

Remarks. This species differs from any described hitherto. The ovoid morphotype superficially resembles *Ctenodonta cambriensis* Hicks from the Arenig of Ramsey Island, which, however, has a length:height ratio approaching two and has less prominent umbones. I have examined Carter's (1971) lectotype of Hicks' species (Manchester Museum MM 10042) and agree that it is a palaeotaxodont. Like much of Hicks' material it is so badly preserved and distorted by cleavage that I recommend restricting the name to the type material. It is impossible to compare the dentition of any of Hicks' material with the Llangynog palaeotaxodonts.

EXPLANATION OF PLATE I

Figs 1–10. *Pensarnia laeviformis* gen. et sp. nov. 1, NMW 78. 17G. 1022, holotype; internal mould of right valve. 2, latex cast of holotype. 3, NMW 78. 17G. 1071; latex cast of left valve. 4, NMW 78. 17G. 1055; right valve, internal mould. 5, NMW 78. 17G. 1051; left valve, internal mould of extremely shortened form. 6, latex cast of specimen shown in fig. 5. 7, NMW 78. 17G. 1060; left valve, internal mould. 8, BGS Geol. Soc. Coll. 6849; left valve, internal mould, figured by Sowerby (*in* Murchison 1839, pl. 22, fig. 1) as *Nucula? laevis*, Roman Road, Pensarn. 9, NMW 78. 17G. 1063; left valve, internal mould, umbo removed to show dentition, posterior end of hinge-plate missing. 10, NMW 78. 17G. 1057; latex cast of left valve external mould. 1–8, 10, $\times 4$; 9 $\times 6.5$.

Figs 11–22. *Paulinea parva* gen. et sp. nov. 11, NMW 78. 17G. 1078, holotype; right valve internal mould. 12, NMW 78. 17G. 1151; left valve, internal mould of shortened form. 13, NMW 78. 17G. 1114; latex cast of left valve. 14, NMW 78. 17G. 1098; right valve, composite mould, showing growth increments. 15, NMW 78. 17G. 1117; enlarged view of gradidentate dentition, right valve, internal mould with umbo removed. 16–17, NMW 78. 17G. 1161; left valve, internal mould and latex cast. 18, NMW 78. 17G. 1172; left valve, internal mould. 19, NMW 78. 17G. 1081; right valve, internal mould of shortened form. 20, NMW 78. 17G. 1164; internal mould, right valve with prominent umbo. 21, NMW 78. 17G. 1091; left valve, internal mould with pronounced growth increment. 22, NMW 78. 17G. 1151; left valve, internal mould, small circular form. 11–14, 16–22, $\times 4$; 15, $\times 6.5$.



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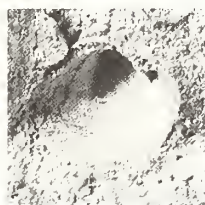
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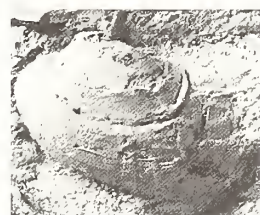
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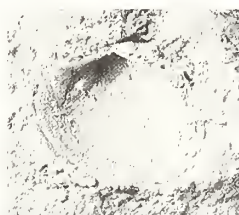
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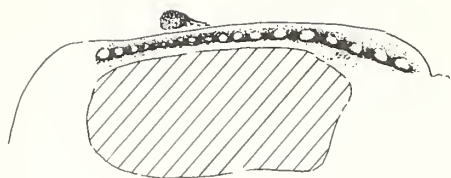
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TEXT-FIG. 3. *Paulinea parva*; NMW 78. 17G. 1161; camera lucida drawing of hinge region of left valve, internal mould. Shaded area is matrix exposed after removal of umbo. Impression of umbo is seen above the hinge line; $\times 10$. Compare with Plate 1, figures 16–17 which are internal mould and latex cast of same specimen before removal of umbo.

Subclass LIPODONTA Cope, 1995

Remarks. The term Lipodonta was originally used by Iredale (1939) at ordinal level. Cope (1995) elevated it to the level of a subclass. Because modern solemyoid and nucinellid forms are protobranch, they have frequently been allied to the other protobranch bivalves, namely the Nuculoida, in the subclass Palaeotaxodonta. However, there are important differences between the two groups including: their shell structure (Taylor *et al.* 1969, 1973), which is unique; a reduced gut in the Lipodonta; a different protobranch gill structure in each group; the Lipodonta also have non-ridged palps and lack the palp proboscides of the Nuculoida. In contrast to the taxodont dentition of the palaeotaxodonts, the majority of lipodontids in which the hinge is known are edentulous. Indeed little seems to unite the two groups except the protobranch gill (as noted by Newell *in* Cox *et al.* 1969, pp. N212–N213). However, as Cope (1995, p. 363) suggested, there now appears good reason to believe that some fossil palaeotaxodonts could have had filibranch gills and so the protobranch condition may not be the diagnostic feature hitherto accepted. Pojeta (1978, 1988) and Pojeta and Runnegar (1985) argued that solemyoids are derived from palaeotaxodonts, and figured anteriorly elongated palaeotaxodonts which are claimed to show the derivation of solemyoids from palaeotaxodonts in the Whiterockian (= Llandeilo). Thus, they claim, both groups should be united in the Palaeotaxodonta. This was also the view of Boss (1982).

The typical solemyoid described below demonstrates that this group was already a separate, fully evolved stock by the early Arenig. Even if they were derived originally from the palaeotaxodonts (a quite reasonable hypothesis) their origins must be pre-Arenig; thus the forms figured and described by Pojeta (1988) must be viewed either as persisting intermediate forms, or as a parallel evolution by palaeotaxodonts during the late mid Ordovician.

Since there are major morphological differences in the soft part anatomy and shell structure and form in these two predominantly protobranch groups, and it is clear that they have been separate since, at latest, earliest Ordovician times, it seems logical to place them in separate subclasses. It seems probable that the separation of the Lipodonta from the Palaeotaxodonta occurred very early in the history of the Bivalvia, but we lack the necessary fossils to link the subclasses. In the *Treatise* (Cox 1969), the solemyoids were placed within the subclass Cryptodonta Neumayr, 1884. However, that subclass has now been discredited as a medley of unrelated forms including pteriomorphians and rostroconchs, amongst others. For this reason, Cope (1995) revived Lipodonta, but as a subclass, which comprises (Cope 1995) one order (Solemyoida Dall, 1889) and two superfamilies. The Solemyoidea Adams and Adams, 1857 includes one family, Solemyidae Adams and Adams, 1857. The Nucinelloidea Vokes, 1956 includes two families: the Nucinellidae Vokes, 1956 and the Manzanellidae Chronic, 1952 (see Pojeta 1988).

Order SOLEMYOIDA Dall, 1889

Superfamily SOLEMYOIDEA Adams and Adams, 1857

Family SOLEMYIDAE Adams and Adams, 1857

Genus OVATOCONCHA gen. nov.

Derivation of name. From the ovoid shape of the shell.

Type species. *Ovatoconcha fragilis* sp. nov.

Diagnosis. Anteriorly elongated bivalve with subdued umbones near posterior end. Straight hinge-line three-quarters length of shell. Shell thin. Large anterior and small posterior muscle impressions. Hinge unknown.

Remarks. The assignation of this rather featureless shell to the Solemyoidea is based on its general overall shape, its muscle scars and the fact that all the specimens seem to be of conjoined valves displaying an anterior and possibly a posterior gape. This suggests that this species may have lived deeply buried in the sediment, away from post-mortem reworking; this is the mode of life of modern solemyoids. The fracturing of the shell appears to be a product of compression, and the pattern of fractures is quite similar to some of those shown by Carboniferous forms figured by Pojeta (1988, pl. 22). Some specimens also show the tracks of radial mantle muscle scars. All solemyoids are of similar shape and form (see illustrations in Pojeta 1988). *Ovatoconcha* appears closest to *Psiloconcha* Ulrich, 1894, but differs in that the umbones are more subdued and the dorsal and ventral margins of the shell are more parallel. Although the specimens are compressed, they appear to have been originally considerably less inflated than *Psiloconcha* (see Pojeta 1988, figures on pls 17–20) and much less so than in *Dystactella* Hall and Whitfield, 1872 (Pojeta 1988, figures on pls 6–10).

The silicification of shells of this species suggests that they originally had a high organic content, as the lingulate brachiopods and the conulariids (which had a high organic content in their shell) are similarly preserved. Modern solemyoids have a thick periostracum and a thin brittle shell with a high organic content to the calcareous parts of the shell (Taylor *et al.* 1969, 1973).

The early Arenig age of *Ovatoconcha* is earlier than the Upper Whiterock age (Llandeilo), for the earliest known species of *Psiloconcha* (*P. senecta* Sardeson, 1896 from the St Peter Sandstone of Minnesota), and it is thus the earliest solemyoid.

Ovatoconcha fragilis sp. nov.

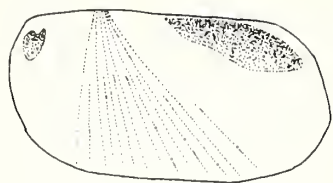
Plate 4, figures 1–2

Derivation of name. From the originally brittle shell.

Material. Five specimens. Holotype: NMW 78. 17G. 1174. Paratypes. NMW 78. 17G. 1175–1178.

Diagnosis. As for genus.

Description. It is assumed that the shell is elongated anteriorly, as in other solemyoids; the umbones thus lie close to the posterior end. The holotype (Pl. 4, fig. 1) is a silicified right valve 17.5 mm long; its height beneath the umbo is 8.7 mm, but the maximum height of 9.6 mm is achieved some 7–8 mm anterior to this point. The umbo is very subdued and appears to be slightly opisthogyral. The surface of the valve is ornamented with fine concentric growth lines; this appears to be the only ornament. Wrinkling of the shell material is believed to be a post-mortem feature. A granulose texture displayed on this specimen is believed to indicate the positions of adductor muscle impressions made visible through compression of the very thin film of silica replacing the shell; these are present as two discrete scars, a small posterior scar and a greatly enlarged anterior scar which extends along the dorsal margin of the valve. Paratype NMW 78. 17G. 1175 (Pl. 4, fig. 2) is somewhat larger (length estimated at 21.5 mm; height below umbones c. 9 mm; maximum height 10.5 mm) and both valves are present. The largely hidden left valve is visible at its anterior extremity and shows clearly that the valves gaped anteriorly. From the umbo and directed obliquely forwards are some ill-defined weak radial ridges; these number eight or nine in the umbonal region, probably twice that number towards the ventral margin of the valve. These radial lines appear to be mantle muscle scars (cf. Pojeta 1988, pl. 22) and are also shown, but not so clearly, by paratype NMW 78. 17G. 1176 (not figured). The intersection of the radial mantle tracks with the growth incremental lines produces an irregular reticulation to the shell which is enhanced by secondary wrinkling of the shell and its subsequent cracking. Paratype NMW 78. 17G. 1175 also shows the muscle impressions well; again a small posterior scar and a much larger anterior scar. None of the material shows the hinge which is presumed to be edentulous.



TEXT-FIG. 4. *Ovatococoncha fragilis*; diagrammatic representation of right valve to show position and shape of adductor muscle scars and tracks of radial mantle muscles. Figure is composite of several specimens; $\times 2$.

Remarks. Since at least three of the five specimens of this species consist of conjoined valves, it appears probable that it may have been deeply infaunal (as are modern solemyoids). The fact that the shells were originally clearly so thin and delicate also lends support to the belief that these forms had a mode of life very similar to that of the modern solemyoids. This material is considerably smaller than that figured by Pojeta (1988).

Subclass PALAEOHETERODONTA Newell, 1965

Order ACTINODONTOIDA Douvillé, 1912

Superfamily GLYPTARCOIDEA superfam. nov.

Diagnosis. Actinodontoids in which the cardinal teeth, instead of radiating out from beneath the umbo, as in the Actinodontoidea, radiate out from a point whose origin is beneath the umbo, but well ventral of the hinge plate and towards the centre of the valves; i.e. the teeth fan out in the opposite direction to that which obtains in the Actinodontoidea.

Remarks. The direction of radiation of the teeth appears to be a fundamental point of distinction between the Glyptarcoidea and the Actinodontoidea. Its significance is that the glyptarcoidean is the type of dentition from which it is easy to derive cyrtodontoid dentition; thus the Glyptarcoidea can be seen as the ultimate origin of the subclasses Pteriomorphia and Neotaxodonta (Cope 1995). Glyptarcoideans could also be derived quite readily from a palaeotaxodont ancestor; the anterior teeth being developed from individual palaeotaxodont teeth and the posterior tooth developing a pseudotaxodont form from an initial single blade-like tooth.

Tironucula Morris and Fortey, 1976 was shown by those authors to develop its taxodont dentition from a juvenile pair of blade-like teeth; they suggested that this developmental pattern implied that palaeotaxodonts could have been derived from actinodontoid ancestors. Pojeta (1978) discussed this feature and the opposite pattern discovered in some Recent palaeotaxodonts by Allen and Sanders (1973), where genera such as *Silicula*, which are clearly of palaeotaxodont origin, develop actinodontoid dentition. The opposing views generated by these forms have fuelled speculation on the nature of the ancestral bivalve dentition.

The early Cambrian *Pojetaia*, with its undoubted palaeotaxodont teeth provides evidence of the antiquity of this type of dentition. Runnegar and Bentley (1983) showed that the mean adult size of *Pojetaia* was only 1.2 mm, and that its hinge was basically similar to that of juvenile specimens of *Tironucula* of the same size. In other words, at extremely small sizes it becomes very difficult to distinguish between actinodont and taxodont dentitions. It is possible that *Tironucula* could be the rule rather than the exception – that early Palaeozoic palaeotaxodont teeth developed ontogenetically from blade-like juvenile teeth – but that this has no implications for the greater antiquity of actinodontoid teeth. Indeed, actinodontoid dentition could be readily derived by paedomorphosis of palaeotaxodont dentition of the *Tironucula* type, so that early actinodontoids could be expected to have two simple blade-like teeth, one anterior and one posterior, and that more complex actinodontoid patterns developed from those. I believe the comparison with the modern protobranchs described by Allen and Sanders (1973) and Sanders and Allen (1973) is wholly inappropriate. Those authors agree that a considerable evolution of the protobranchs has taken place in the deep sea; presumably protobranchs have survived in such variety there because of the ready availability of food for deposit feeders, and reduced competition from other bivalves. Appraisal of the dentition of these forms shows that when they are pseudo-actinodontoid, the

ligament is still to be found centrally on the hinge plate beneath the umbo. This I believe is of high significance, because palaeotaxodont bivalves had external ligaments until the Silurian (Pojeta and Runnegar 1985) and it is not until then that the ligament becomes internal and housed centrally on the hinge-plate. This differs considerably from actinodonts, which had an external opisthodontic ligament. Thus the dentition of these modern deep-sea non-taxodont protobranchs can logically be interpreted as being secondarily derived from a palaeotaxodont dentition which has a central resilifer; this means that the derivation could not date from further back than early Silurian (in fact it appears likely to be of much later origin and to date from the major deep-sea radiation of the protobranchs in the Mesozoic and Cenozoic).

It could be argued that the glyptarcoideans, with their teeth radiating in the opposite direction to those of the actinodontoideans, are more remotely related to them than at superfamilial level. However, both actinodontoideans and glyptarcoideans have types of dentition which could be readily derived from palaeotaxodont ancestors and both these groups gave rise to forms which have filibranch gills. It therefore seems probable that the Actinodontoida had filibranch gills, as the development of a feeding gill from the protobranch condition is unlikely to have arisen more than once; I therefore draw the parsimonious conclusion that the Actinodontoida is monophyletic and that both its superfamilies had filibranch gills. Allen and Sanders (1969) suggested that the Actinodontoida were probably protobranchs; this was based on their view that the solemyoid *Nucinella* was a living actinodont. However, Pojeta (1988) has shown that *Nucinella* has its umbones at the posterior and is elongated anteriorly; the lateral teeth are entirely anterior and they are separated by an edentulous space from the subumbonal taxodont teeth. In all these features it differs fundamentally from the actinodontoids.

Family GLYPTARCIDAE nov.

Diagnosis. As for superfamily, as this is the only family yet recognized.

Remarks. This new family is proposed to include *Glyptarca* Hicks, 1873 and the species described as *?Dolabra lusitanica* Sharpe, 1853, and revised by Babin and Gutiérrez-Marco (1991) who referred it with question to *Glyptarca*, which they pointed out was poorly defined. However, it is now possible to define *Glyptarca* precisely with a formal full diagnosis, and it is clear that '*?Dolabra lusitanica*' requires a new generic assignation, for which *Hemiprionodonta* is proposed, with '*?D. lusitanica*' as type species. I agree with Babin and Gutiérrez-Marco (1991) in assigning *Arca naranjoana* Verneuil and Barrande, 1856 to this species. Another species, brought to my attention by Mr S. P. Tunnicliff, which clearly belongs to *Hemiprionodonta* is *Palaearca* (*Matheria*?) *quadrata* Salter, 1866 (p. 343, woodcut 12, fig. 3) from the Caradoc of North Wales. *Hemiprionodonta lusitanica* was fully described and illustrated by Babin and Gutiérrez-Marco (1991, text-figs 6–7). It differs from *Glyptarca* species in having a somewhat different dentition in which the anterior teeth are not a continuous group, which Babin and Gutiérrez-Marco separated into two anterior pseudolaterals and two pseudocardinals; the latter do not overlap the posterior lateral tooth to any significant degree. *H. lusitanica* also has rounder and generally more deeply impressed adductor scars than *Glyptarca* species, and is significantly larger. *Hemiprionodonta* is clearly related to *Glyptarca*, and belongs to the same family; it may even be a direct descendant of *Glyptarca*, being somewhat younger stratigraphically.

Genus GLYPTARCA Hicks, 1873

Type species. Subsequently designated by Newell 1969: *Glyptarca primaeva* Hicks, 1873.

Diagnosis. Carinate bivalve with anterior set of at least four teeth overlapping posterior teeth subumbonally. Posterior teeth anteriorly separate or pseudotaxodont, posteriorly pseudotaxodont or lamellar.

Remarks. *Glyptarca* was founded by Hicks (1873, p. 48) for *G. primaeva*, which occurs abundantly on Ramsey Island and at Tremanhir in Pembrokeshire (south-west Dyfed). I have examined all the syntype and topotype material in the collections of the British Geological Survey, the Sedgwick Museum and the Manchester Museum. Hicks' description mentions three teeth anterior to the umbo; this is shown unequivocally only by one syntype, a somewhat distorted specimen (BGS GSM 24200) figured by Hicks (1873, pl. 5, fig. 2) and by Carter (1971, pl. 38, fig. 14). The lectotype, (Carter 1971, pl. 38, fig. 8) appears to me to be an unfortunate choice, as it is an external mould and does not show the dentition. Some syntypes show the single posterior tooth, but the majority show no trace of dentition; this is probably a vagary of preservation – much of the Ramsey Island material is badly distorted by cleavage and it is likely that the valve has been sheared over the hinge plate, thus making it invisible. This seems to have occurred regularly with specimens of *Glyptarca*, but often on the same slabs there are occasional palaeotaxodont bivalves with dentition preserved, though distorted. This difference in preservation seems due to the hinge plate being well beneath the dorsal margins of the valves in *Glyptarca* whilst it is not so far beneath them in the palaeotaxodonts. I prefer this interpretation to the alternative, that there are two genera represented by Hicks' syntypes of *G. primaeva*, a toothed form and an edentulous form. I thus interpret the lectotype as a form with a hinge plate which has been effectively obliterated by crushing/shearing of the valve over it. It forms far from ideal material on which to found a genus and some further action is needed if the name is to be preserved as a useful taxonomic entity. No Ramsey Island material of *Glyptarca* appears to exist which has completely preserved dentition. In an attempt to stabilize the nomenclature, I have assumed that the lectotype belongs to the same species as the paralectotype figured by Carter (1971, pl. 38, fig. 14). In order to allow a better interpretation of the genus, a new species of *Glyptarca* is described below which has perfectly preserved dentition. The poor preservation of the Ramsey Island material allowed Hicks only to give an inadequate description of *G. primaeva*.

Carter (1971, p. 259) believed that *Glyptarca* was not included in the *Treatise* (Cox *et al.* 1969), but it is included on p. N256 as a synonym of *Parallelodon*, where Newell designated the type species (by monotypy), making Carter's (1971, p. 258) designation invalid. Newell's designation was also overlooked by Babin and Gutiérrez-Marco (1991). The reference in the *Treatise* may have been inserted at a late stage, as it follows the description and figure references, and it is omitted from the index. The dentition, described fully below (under *G. serrata* sp. nov.) shows that *Glyptarca* is not a *Parallelodon*, but is a palaeoheterodont, and is clearly not related to the modiomorphoid genera *Byssoderma* Isberg, 1934 or *Colpomya* Ulrich, 1894 as Carter (1971, p. 259) suggested it might be.

EXPLANATION OF PLATE 2

Figs 1–11. *Glyptarca serrata* sp. nov. 1, NMW 78. 17G. 801, holotype; left valve, internal mould. 2, NMW 78. 17G. 691; left valve, internal mould of small shortened form. 3, NMW 78. 17G. 519; left valve, composite mould. 4, NMW 78. 17G. 550; left valve internal mould, showing non-crenulated posterior end of posterior tooth. 5, NMW 78. 17G. 701; small left valve, internal mould, with posterior tooth entirely fused, but showing crenulations. 6, NMW 78. 17G. 795; internal mould of right valve showing carinate posterior shoulder. 7, NMW 78. 17G. 821; left valve, internal mould showing fused posterior portion of tooth. 8, NMW 78. 17G. 685; latex cast of external mould. 9, NMW 78. 17G. 606; right valve, internal mould. 10, NMW 78. 17G. 490; enlarged view of right valve internal mould with umbo removed, to show overlap of anterior and posterior dentition in subumbonal region. 11, NMW 78. 17G. 540; enlarged view of right valve as in fig. 10. 1–9, $\times 4$; 10–11, $\times 6.5$.

Fig. 12. *Fortowensia grandis* gen. et sp. nov.; NMW 78. 17G. 1192; latex cast of holotype; left valve, internal mould. cf. Pl. 6, fig. 4; $\times 2.8$.

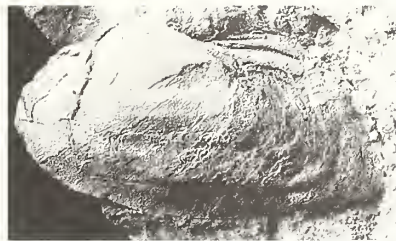
Fig. 13. *Celtoconcha foveata* gen. et sp. nov.; NMW 78. 17G. 1218; poorly preserved internal mould of right valve showing muscle scars and vertical muscle tracks; $\times 4$.



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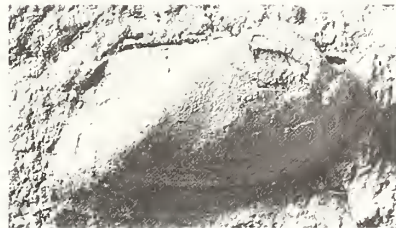
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Glyptarca serrata sp. nov.

Plate 2, figures 1–11

Derivation of name. From the serrated appearance of the posterior lateral tooth.

Material. 484 specimens (218 LV, 201 RV, 65 CV). Holotype: NMW 78. 17G. 801. Paratypes: NMW 78. 17G. 448–800; 78. 17G. 802–931.

Diagnosis. Small to medium-sized (up to 14.4 mm long) elongate bivalve with four to nine anterior teeth arranged in a radially divergent pattern with centre of radius towards middle of valves. Anterior teeth overlap posterior tooth in central region of hinge-plate; posterior tooth in juveniles single and blade-like in each valve, but developing division into separate peg-like teeth as in palaeotaxodonts in mature forms.

Description. The specimens are 3.4–14.4 mm long and 2.2–7.7 mm high. A plot of length against height for the material shows a fairly continuous spread of points and it seems probable that various growth stages are represented. As the larger specimens show the dentition far better, specimens predominantly towards the larger end of the size range are figured herein.

The holotype shows the dentition well, although it is impossible to see the complex dental arrangement beneath the umbonal region; for this reason some specimens have been prepared by carefully removing the umbonal areas of the internal moulds so that details of the dentition become visible. The holotype is a left valve 11.6 mm long and 7.5 mm high. The external mould shows the exterior to be ornamented solely by growth lines which become most pronounced at the ventral part of the carina-like ridge which extends posteriorly from the umbo. The internal mould is not complete as the posterior end is broken away, but it shows most of the characteristic features of the species. The anterior adductor muscle impression is impressed very shallowly and is heart-shaped; lying adjacent to it in a dorsal position is a narrow triangular impression, presumably of a pedal retractor muscle. The posterior adductor is approximately the same size as the anterior, but is of roughly circular shape. The paratypes commonly show neither adductor scar, and both are, at best, only very shallowly impressed. The pallial line is not deeply impressed either; it is invisible on the holotype, but several paratypes show it to have been entire.

Impressions corresponding to five anterior teeth are visible on the holotype; others may be present beneath the umbo. The most anterior tooth reaches almost to the anterior margin of the valve and is slightly curved. In some paratypes (e.g. Pl. 2, fig. 11) there is pronounced curvature of this tooth. The remainder of the anterior teeth are radially disposed, with the centre of the radius lying towards the centre of the valve. Paratype NMW 78. 17G. 540 (Pl. 2, fig. 10) has had its umbo removed to show the dentition which includes a row of eight anterior teeth, rapidly diminishing in size posteriorly. On the holotype the second most anterior tooth bears fine longitudinal grooves, whilst paratype NMW 78. 17G. 550 (Pl. 2, fig. 4) has horizontal striations on its most anterior tooth; these exceptions apart, the teeth appear entirely smooth. The long posterior lateral tooth is arched to follow closely parallel to the dorsal margin of the valve. The anterior end of this is subdivided into several discrete teeth, and at least three of these are entirely free on the holotype. Paratype NMW 78. 17G. 550 appears to show about nine discrete teeth. Posterior to this the tooth appears to be a fusion of many separate peg-like teeth; in some the anterior end of the posterior lateral tooth may be divided into as many as 14 separate teeth, whilst others have the entire row fused. In this latter case, however, a crenulation is visible at the anterior end, showing a pseudo-separation. The subdivision of this tooth may largely be a function of size or maturity, as the smaller specimens show little or no such separation, merely a single tooth. One of the most distinctive features about the dentition of *Glyptarca serrata* is that the anterior and posterior rows of teeth overlap significantly beneath the umbones, the anterior teeth lying below the posterior. This feature is, however, not visible unless the umbones are removed from the internal moulds.

Remarks. This species is clearly closely related to *Glyptarca primaeva* Hicks, from which it may be distinguished readily by its lack of a median sinus. This feature appears to be real and not just a vagary of distortion. Within Hicks' type material of *G. primaeva* there is at least one specimen (BGS GSM 24199) which may be referred to *G. serrata*; it is on a small slab measuring some 35 mm square, with over 40 small bivalves, most of which are featureless. The slab was labelled '*Glyptarca primaeva*' by Hicks, and contains at least one palaeotaxodont and many small bivalves lacking a



TEXT-FIG. 5. *Glyptarca serrata*; camera lucida drawing of hinge region of internal moulds to show details of subumbonal overlap of the two sets of teeth. Shaded areas indicate matrix exposed after removal of umbones. Impressions of umbones may be seen above the hinge line. A, NMW 78. 17G. 490; right valve. B, NMW 78. 17G. 540; left valve. Both $\times 5$.

median sulcus, and one specimen with a crenulated posterior tooth which is referable to *G. serrata*. However, none of Hicks' material of *G. primaeva* is well enough preserved to show the subumbonal dentition, even if the umbones were removed. Many of the characters of the genus are thus best displayed by *G. serrata*, and my intention here is to stabilize the generic name by providing an adequate diagnosis and description of better preserved material.

The overlapping dentition of *Glyptarca* is a rare feature in bivalves, and I have been able to find it in only two other genera: the palaeotaxodonts *Cardiolaria*, from the middle Ordovician, and some Jurassic species of *Palaeoneilo* (see Cox 1937). To find that two of the three genera possessing this distinctive dentition are of very similar age strongly suggests that they could be phylogenetically linked. Cope (1995, p. 363) proposed that such forms could provide a link between palaeotaxodonts and palaeoheterodonts.

Superfamily ACTINODONTOIDEA Douvillé, 1912

Diagnosis. Actinodontids with teeth radiating out ventrally from beneath the umbo.

Remarks. This superfamily includes all the non-glyptarcoidean actinodontians, and ranges from Tremadoc to late Devonian (assuming the families Carydiidae and Babinkidae are actinodontoids). The type species of *Actinodonta*, *A. cuneata* Phillips, 1848, is from the Upper Llandovery of Marloes Bay, Pembrokeshire (Dyfed), but Pojeta (1971) recorded it incorrectly from the middle Ordovician of Britain and designated one of Phillips and Salter's specimens (1848 pl. 21 fig. 2) as the lectotype. A lectotype had, however, been already designated (Stubblefield 1938) making Pojeta's designation invalid. However, both authors chose the same specimen (BGS GSM 59825).

Family CYCLOCONCHIDAE Ulrich, 1894

Remarks. The Cycloconchidae, as here restricted, embraces a group of closely allied genera in which the subumbonal teeth (pseudocardinals of Pojeta and Runnegar 1985) are in general much shorter and at high angles to the hinge when compared with the longer pseudolaterals (Pojeta and Runnegar 1985). However, in some forms there is a gradual lengthening of the posterior pseudocardinals, so that in some cases they merge imperceptibly into the pseudolaterals and it is difficult to separate the two.

The following genera are included: *Cycloconcha* Miller, 1874; *Actinodonta* Phillips, 1848; *Copidens* Pojeta and Gilbert-Tomlinson, 1977; *Ananterodonta* Babin and Gutiérrez-Marco, 1985; *Carminodonta* gen. nov., *Fortowensia* gen. nov. and *Celtoconcha* gen. nov. *Catamarcaia* Sánchez and Babin, 1993 may also belong, although those authors placed it in the Arcoida. However, it has a typical cycloconchid dentition which differs fundamentally from the arcoid type in lacking a subumbonal edentulous area; its one pteriomorph feature is the grooved ligamental area, but, as shown by Waller (1978), this may reflect an entirely lamellar ligament and not indicate a duplivincular condition. It does, however, suggest that the grooved ligamental area may have first

arisen in the palaeoheterodonts, and the condition was then acquired by the cyrtodontoids. *Babinka* Barrande, 1881 was regarded by McAlester (1965, 1966) as a lucinoid heterodont; however, as discussed by Cope (1995, p. 366), because of its early appearance (range Tremadoc–Llanvirn) I prefer to regard it as a palaeoheterodont, and it may well be a cycloconchid in which the lateral teeth have been suppressed.

The genera which constitute the Cycloconchidae are a closely related group. *Carminodonta*, *Fortowensia* and *Celtoconcha*, from the lower Arenig, are amongst the earliest known members. *Catamarcaia* is from the upper Arenig, whilst *Copidens* is known from the Nora Formation of Australia which is dated as probably around the early–mid Ordovician boundary (Pojeta and Gilbert-Tomlinson 1977, p. 5). *Ananterodonta* is from the lower Llanvirn, whilst *Cycloconcha* is of mid–late Ordovician age and *Actinodonta* seems restricted to the lower Silurian. However, there are many references to this latter genus from the Ordovician, including one of Hicks' species from Ramsey Island. *Modiolopsis ramseyensis* was quoted by Carter (1971, p. 258) as being 'indistinguishable from *Actinodonta cuneata* Phillips'. I have examined Hicks' holotype of *M. ramseyensis* (Manchester Museum L10041) and found that its length is 22.8 mm as opposed to the 28 mm Carter records; its height is 10.3 mm (not 9 mm) and, although the specimen is quite distorted, the single long posterior tooth is the sole visible dentition and is quite unlike a cycloconchid. As Carter (1971, p. 250) remarked, most of Hicks' material should never have been named and in this case too the name should be restricted to the type material. Other examples of *Actinodonta* from the Ordovician can also now probably be referred to other genera. Pojeta and Gilbert-Tomlinson (1977, p. 4) have suggested that some of the specimens from the Grès Armoricaïn that Barrois (1891) referred to *Actinodonta* could belong to *Copidens*. Other generic assignments remain to be made, and most of the earlier references to *Actinodonta* seem to have been made by reference to one of the syntypes of *A. cuneata* figured by Phillips (1848), particularly his plate 21, figure 4, which came from the Wenlock (given as Lower Ludlow by Stubblefield 1938) and would now almost certainly be assigned to a separate genus following the stabilization of the nomenclature by the lectotype designation of Stubblefield (1938).

Davidia Hicks, 1873 was included in the Cycloconchidae by Morris (1978). However, as discussed below, Hicks' type material is totally uninterpretable and the figure of its cycloconchid dentition produced by Morris (1978, fig. 25) thus cannot belong to that genus. Regrettably this error was perpetuated by Pojeta and Runnegar (1985, p. 322). Morris' assignment of Barrois' species *Actinodonta carinata* to *Davidia* has been the cause of this confusion.

Genus CARMINODONTA gen. nov.

Derivation of name. From the comb-like organization of the hinge teeth.

Type species. *Carminodonta crossi* sp. nov.

Diagnosis. Elongate prosogyral cycloconchid, with pronounced shoulder from umbo to postero-ventral margin; shell terminated abruptly posteriorly. Radiating sheaf of eight to eleven pseudocardinal teeth elongating posteriorly into four or five pseudolaterals all borne on a hinge plate; one short or no anterior pseudolaterals. Anterior teeth not persisting to anterior end of hinge-line.

EXPLANATION OF PLATE 3

Figs 1–6, 8. *Carminodonta crossi* gen. et sp. nov. 1, NMW 78. 17G. 1185; left valve, internal mould. 2, NMW 78. 17G. 1179, holotype; left valve, internal mould. 3, NMW 78. 17G. 1182; latex cast of external mould of left valve. 4, latex cast of holotype as fig. 2. 5–6, NMW 78. 17G. 1180; latex cast and internal mould of left valve. 8, NMW 78. 17G. 1183; external mould of left valve, showing attached hinge-plate. All $\times 3$.
Fig. 7. *Modiolopsis* sp. B; NMW 78. 17G. 1231; $\times 2$.



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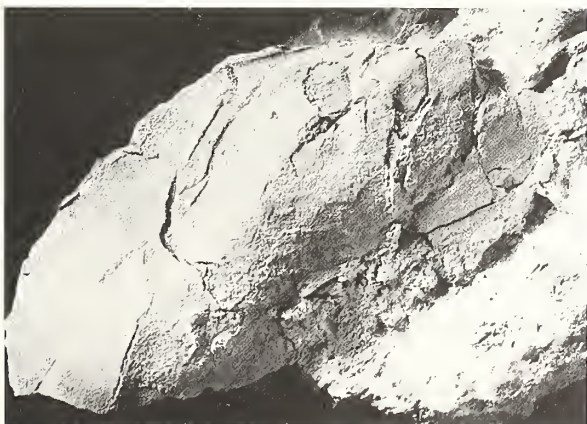
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Remarks. *Carminodonta* is distinguished from other cycloconchids by its dentition and shape. It is closest to *Actinodonta*, but may be readily distinguished from it by its overall shape, in particular by the posterior end of the shell which is abruptly truncated in *Carminodonta*, and tapers in *Actinodonta*. There are also significant differences in the dentition; the anterior teeth do not reach the anterior end of the hinge-line in *Carminodonta*, whereas in *Actinodonta* the teeth continue right to its anterior end. This was demonstrated best by Pojeta (1978, pl. 4) who figured latex replicas of both the lectotype (a left valve) and a right valve paralectotype (compare with Pl. 3, figs 4–5, 8). *Copidens* is distinguished from *Carminodonta* by its circular outline, the gradual increase in length of the teeth posteriorly, the proximity of its anterior adductor to the hinge-plate, and the lack of any posterior shoulder to the shell.

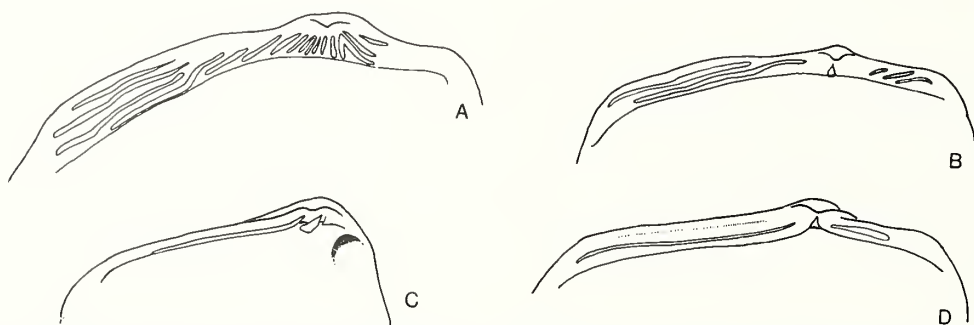
Carminodonta crossi sp. nov.

Plate 3, figures 1–6, 8

Derivation of name. For Mr F. R. B. Cross, formerly Chief Technician, Department of Geology, University College, Swansea, in acknowledgement of his assistance in the field and laboratory for many years.

Material. 13 specimens (8 LV, 4 RV, 1 CV). Holotype: NMW 78. 17G. 1179. Paratypes: NMW 78. 17G. 1180–1191.

Diagnosis. As for genus.



TEXT-FIG. 6. Diagrammatic representation of dentitions of left valves of the new actinodontoidean genera. A, *Carminodonta crossi*; $\times 4$. B, *Celtoconcha foveata*; $\times 4$. C, *Moridunia simplicidens*; $\times 3$. D, *Fortowensia grandis*; $\times 2$.

Description. The holotype is a left valve approximately 17.9 mm long (its posterior extremity is damaged) and 9.8 mm high; the maximum height is achieved slightly posterior of the umbo. Paratype NMW 78. 17G. 1180 (Pl. 3, fig. 6) shows the posterior end of the shell well and it can be seen to be obliquely truncated. Anterior and posterior adductor muscle scars are equally shallowly impressed; the anterior one is circular, the posterior being somewhat the larger and subcircular to scutate in shape. There is a well impressed anterior pedal retractor scar dorsal to the anterior adductor, particularly well shown by paratype NMW 78. 17G. 1181. The same specimen appears to show a faint pallial muscle impression, but this is not visible on any of the other material.

The exterior of the shell is shown by several paratypes, most of which are somewhat distorted. However, NMW 78. 17G. 1182 (Pl. 3, fig. 3), the best preserved, shows that the shell is ornamented by faint growth lines; towards the posterior end some of these are strengthened to form commarginal rugae. There is a marked shoulder running from the umbo to the postero-ventral margin, which is, however, not sharp enough to be termed a carina. One of the less well preserved specimens has a suggestion of a fine radial ornament which appears to be restricted to the posterior extremity of the shell.

The dentition is well shown by the holotype and several of the paratypes. It conforms to the same style in all the material. In the holotype the distinction between pseudocardinal and pseudolateral teeth is difficult to make as the posterior pseudocardinals merge into the anterior pseudolaterals. However, the holotype shows one clear anterior pseudolateral which lies parallel to the hinge; although it arises close to the pseudocardinal cluster it appears to be separated from it. Immediately posterior to this is a sheaf of ten teeth which radiate from the same point and which all appear to be dorsally united; these constitute the pseudocardinal cluster. Lying adjacent to and parallel with the posterior pseudocardinal tooth is the most anterior of the five posterior pseudolateral teeth; the two anteriormost are short, the others longer. The paratypes show a similar style of dentition, although none shows an anterior pseudolateral tooth. The number of pseudocardinal teeth varies from about eight up to eleven.

Dorsal to the posterior pseudocardinal teeth and the anterior two of the posterior pseudolaterals, the holotype bears a shallow impression which may even be a vagary of the preservation, but which may be the site of an external opisthodontic ligament.

Remarks. This is one of the rarer members of the Llangynog fauna, but is so distinctive that it can be recognized even with incomplete material, providing that the dentition is, at least in part, preserved. Similar rarity seems to apply to other genera in this group, *Ananterodonta* being known from only one specimen. In the case of the Llangynog fauna, *Carminodonta* constitutes less than 1 per cent. of the bivalve fauna.

Genus FORTOWENSIA gen. nov.

Derivation of name. After Drs R. A. Fortey and R. M. Owens, in recognition of their work on the Arenig Series.

Type species. *Fortowensia grandis* sp. nov.

Diagnosis. Elongate cycloconchid with a single pseudocardinal tooth in each valve and with one anterior and one posterior pseudolateral in the left valve; two of each in the right valve.

Stratigraphical range. Known only from the lower Arenig.

Remarks. The dentition and shape of this genus render it readily distinguishable from other palaeoheterodonts in the Llangynog fauna. Superficially it resembles the specimens of *Parallelodus* described below, but this is merely due to their similarity in size, and the two genera differ fundamentally in their shape and dentition. These same characters also serve to distinguish it from other palaeoheterodont genera; the reduced dentition separates it from other cycloconchids, but its shape is quite different from redoniids, and also actinodontoids with reduced dentition. It also differs from redoniids in lacking a deeply inserted anterior adductor with myophoric buttress.

Fortowensia grandis sp. nov.

Plate 2, figure 12; Plate 6, figures 3–4

Derivation of name. From the Latin *grandis* (= large). This is one of the largest bivalves of the fauna.

Material. 20 specimens (8 LV, 6 RV, 6 CV). Holotype: LV NMW 78. 17G. 1192. Paratypes: NMW 78. 17G. 1193–1211.

Diagnosis. *Fortowensia* c. 30 mm in length. Other characters as for genus.

Description. The holotype is approximately 29 mm long (the posterior extremity is broken) and 18.2 mm high. The anterior adductor muscle is shallowly impressed, but is just visible as a circular scar at the anteriormost part of the shell; the posterior adductor is not visible in most specimens. The umbones, although well-developed, arise gradually from the dorsal part of the valve. There is a single pseudocardinal tooth in each valve; on the holotype this appears to rise from beneath the umbonal region. The hinge-line is straight and

there is a single long posterior lateral tooth in the left valve and two posterior lateral teeth in the right valve. There is a single anterior pseudolateral in the left valve and two in the right; both of these are short and closely parallel to the dorsal margin of the valves. The more posterior of the anterior pseudolaterals in the right valve arises close to the pseudocardinal tooth; its course is initially parallel with the pseudocardinal tooth, but then swings forward to be parallel with the dorsal margin.

Paratype 78. 17G. 1193 (Pl. 6, fig. 3) shows the posterior adductor muscle impression; it is considerably larger than the anterior scar, is rounded posteriorly but sharply triangulate towards its anterior origin. This specimen also shows well the posterior end of the shell, which is inclined gently back from the posterior end of the hinge line and rounded. A further feature shown by the same paratype is pallial punctae (extra pallial muscle impressions also found in other members of this fauna, particularly in *Falcatodonta*, described below).

Remarks. The size of *F. grandis* (length 25–c. 35 mm; the posterior extremity is missing on the longest specimen) is quite usual amongst Llanvirn or later faunas, but not in the early Arenig, when it was shared only by a few modiomorphoids, from which it is readily distinguished by its dentition and shape.

Genus CELTOCONCHA gen. nov.

Derivation of name. After the former inhabitants of Wales.

Type species. *Celtoconcha foveata* sp. nov.

Diagnosis. Strongly inflated quadrate to subquadrate postero-ventrally extended cycloconchid with single pseudocardinal tooth in left valve, and well-developed anterior and posterior pseudolateral teeth. Multiple pedal muscle insertion scars often prominent sub-umbonally.

Stratigraphical range. Known only from the Moridunian Stage, lower Arenig.

Remarks. This genus has reduced dentition in comparison with other members of the Cycloconchidae, as the pseudocardinal teeth are reduced to one in the left valve and only the single corresponding socket in the right valve. However, both anterior and posterior pseudolaterals are well-developed and there can be no doubt of the familial assignment; the teeth are certainly not reduced sufficiently to merit placement of *Celtoconcha* within the Redoniidae. When compared with other cycloconchids, the closest similarity is with *Cycloconcha*, but the anterior pseudolaterals are longer, and can be separated readily from the single pseudocardinal, whereas in *Cycloconcha* the two are not readily separable (e.g. see Pojeta and Runnegar 1985, fig. 13A). The other point in common with *Cycloconcha* is the multiple pedal muscle scars. The overall shape of the shell contrasts

EXPLANATION OF PLATE 4

Figs 1–2. *Ovatoconcha fragilis* gen. et sp. nov.; silicified composite moulds. 1, NMW 78. 17G. 1174, holotype; right valve displaying granulose texture over area of large anterior adductor. 2, NMW 78. 17G. 1175; conjoined valves, displaying right valve showing radial mantle muscle scars and large anterior adductor, much smaller posterior adductor partly visible. Both $\times 3$.

Figs 3, 5. *Goniophorina* (*Cosmogoniophorina*) *extensa* sp. nov. 3, NMW 78. 17G. 1227; latex cast of external mould of left valve. 5, NMW 78. 17G. 1222, holotype; right valve, internal mould. Both $\times 3.5$.

Figs 4, 7–8. *Celtoconcha foveata* gen. et sp. nov. 4, NMW 78. 17G. 1217; badly distorted right valve showing marked discrete pedal muscle scars; $\times 4.5$. 7, NMW 78. 17G. 1215; left valve, internal mould; three pedal muscle scars just visible to posterior of umbo pointing to postero-ventral margin; $\times 3.5$. 8, NMW 78. 17G. 1212, holotype; right valve, internal mould, lit to show pedal muscle scars; $\times 3.5$.

Fig. 6. *Cyrtodontula* cf. *hadzeli* Pojeta and Gilbert-Tomlinson, 1977; NMW 78. 17G. 1234; left valve, internal mould; $\times 2$.

Fig. 9. *Cleionychia* sp.; NMW 78. 17G. 1269; composite mould of left valve; middle Arenig, Whitlandian Stage, Llangynog; $\times 2$.



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markedly, however, with the circular shape of *Cycloconcha*, as do the very strongly inflated valves of *Celtoconcha*. It is possible that *Celtoconcha* has a common ancestry with *Cycloconcha*, as both share the character of multiple pedal muscle insertions.

Celtoconcha foveata sp. nov.

Plate 2, figure 13; Plate 4, figures 4, 7–8

Derivation of name. From the scars of the multiple pedal muscle insertion points.

Material. Ten specimens (4 LV, 6 RV). Holotype: RV NMW 78. 17G. 1212. Paratypes: NMW 78. 17G. 1213–1221.

Diagnosis. As for genus.

Description. The holotype (Pl. 4, fig. 8) is a well-preserved, largely undistorted, internal mould of a right valve. It is 15.0 mm long and 9.9 mm high, but the postero-ventral margin of the valve (where the height is greatest) is missing. The postero-ventral angle is, however, well displayed by paratype NMW 78. 17G. 1214, in which it is quite acute and posteriorly extended. Left valve features are well shown by paratype NMW 78. 17G. 1215 (Pl. 4, fig. 7), which is 15.2 mm long and 12.2 mm high. The shell is quadrate to subquadrate in outline and is strongly convex. The exterior of the shell is displayed by the three external moulds, none of the which is complete; however, they show that the shell was essentially smooth, the only ornamentation being fine growth increments towards the ventral margin. The umbo is just anterior of central on the hinge-line and is orthogyrate. Beneath the umbo is a narrow single right valve pseudocardinal socket and, immediately anterior to this, one or two anterior pseudolateral teeth arise in the right valve, two or three in the left. There are two posterior pseudolaterals in the left valve, but only one in the right valve. The anterior of the left valve posterior pseudolaterals is the shorter; in addition to being longer, the other more closely parallels the dorsal margin of the valve. The posterior of the shell is abruptly truncated by a sharp angular change at the posterior end of the hinge-line. No specimen shows adductor muscle scars or pallial line, but there is a series of well-defined muscle scars running across the dorsal side of the shell which are presumably pedal retractor muscle impressions. There are five (and possibly a sixth) on the holotype; paratypes NMW 78. 17G. 1215–1217 are all distorted at this area of the shell, but each shows at least two scars. Paratype NMW 78. 17G. 1218 (Pl. 2, fig. 13), which is a poorly preserved internal and external mould, shows vertical tracks associated with some of these accessory muscle scars. The external mould of this specimen is very poorly preserved, but suggests that the only ornament present is fine growth increments.

Remarks. Similar accessory muscle scars to those of *C. foveata* occur in a *Cycloconcha* figured by Pojeta (1971, pl. 2, figs 8–9). A reconstruction by Pojeta and Runnegar (1985, fig. 13) shows seven accessory scars.

EXPLANATION OF PLATE 5

Fig. 1. *Xestoconcha* sp.; NMW 78. 17G. 1238; latex cast from internal mould of left valve, showing dentition; $\times 3$.

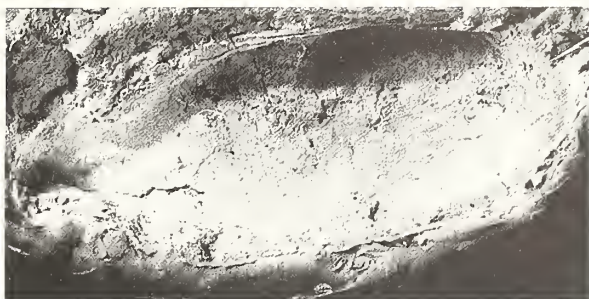
Figs 2–3. *Parallelodus dyfedensis* sp. nov.; NMW 78. 17G. 1233, holotype; latex cast and internal mould; $\times 2$.

Figs 4–11. *Moridunia simplicidens* gen. et sp. nov. 4, NMW 78. 17G. 161, latex cast of holotype; left valve, showing dentition and musculature; note prominent central tooth. 5–6, NMW 78. 17G. 387; internal mould and latex cast of large left valve. 7, NMW 78. 17G. 111; hinge region of latex cast of left valve. 8, NMW 78. 17G. 164; latex cast of right valve, showing apparent gap in hinge-plate, which is a very deep socket corresponding to central left valve cardinal tooth; note how tooth posterior to this socket bends round to posterior lateral attitude. 9, NMW 78. 17G. 359; hinge region of latex cast of a quadrate form showing more acute angle in hinge-plate. 10, NMW 78. 17G. 163; small right valve internal mould. 11, NMW 78. 17G. 170; latex cast of exterior mould of right valve showing commarginal ornamentation. All $\times 3$.

Fig. 12. *Cyrtodonta* cf. *staffordae* Pojeta and Gilbert-Tomlinson, 1977; NMW 78. 17G. 1240; right valve, internal mould; $\times 2$.



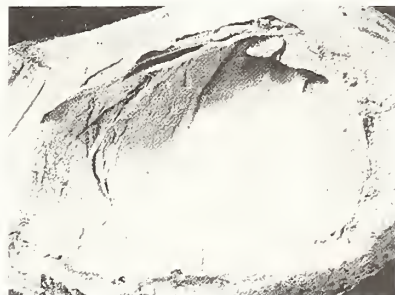
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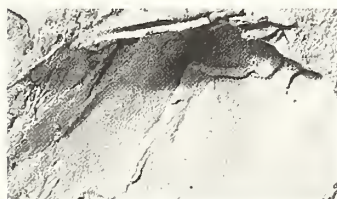
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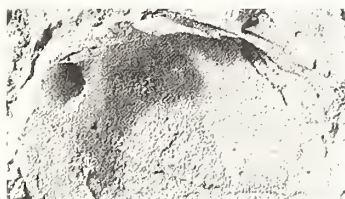
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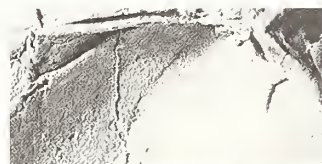
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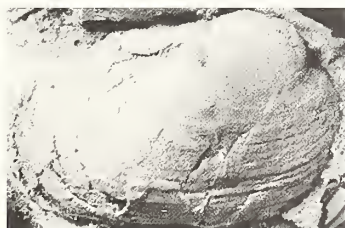
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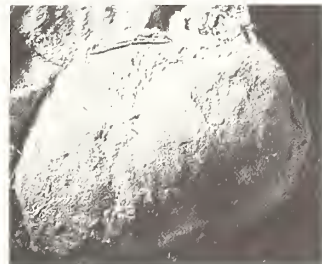
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Family REDONIIDAE Babin, 1966

The redoniids are actinodontoideans with a much reduced dentition. The umbo is well to the anterior end of the shell and the hinge-plate has one or two pseudocardinal teeth and one or two posterior pseudolaterals; the teeth may be smooth or microcrenulated. The anterior adductor muscle is very strongly impressed with a variably developed myophoric buttress delimiting its posterior margin. Included are: *Redonia* Roualt, 1851, *Dulcineaia* Babin and Gutiérrez-Marco, 1991, and *Moridunia* gen. nov. Their reduced dentition readily distinguishes them from other actinodontoideans.

Remarks. *Moridunia* is of a similar early Arenig age as the hitherto earliest known redoniid (*Redonia michelae* Babin) from the Montagne Noire and the Moroccan Anti-Atlas, and is interesting in that it shows development of redoniid features, but not to the same extent as in the other genera.

Genus MORIDUNIA gen. nov.

Derivation of name. From the Roman fort of Moridunum, now Carmarthen.

Type species. *Moridunia simplicidens* sp. nov.

Diagnosis. Redoniid with prominent, though not pointed, beak a little back from anterior extremity, anterior adductor well impressed with shallow myophoric buttress to posterior. Single central pseudocardinal tooth in left valve; right valve with blunt anterior pseudocardinal and elongated posterior pseudocardinal. One elongate posterior pseudolateral tooth in each valve. Shells with shallow ligamental nymphs locating opisthodontic ligament.

Range. Known only from the early Arenig.

Remarks. *Moridunia* has dentition most closely resembling that of *Redonia*, with which it shares a well-impressed anterior adductor muscle but with a shallow myophoric buttress. It is also distinguished by the more elongate shape and less prominent umbones. It lacks the ridged teeth of *Dulcineaia*. An apparent similarity in dentition to *Allodesma* Ulrich, 1894 is probably superficial. The figures of that genus in the *Treatise* (Cox *et al.* 1969, p. N400, fig. D8, 3a–b) are taken directly from Ulrich's figures. Pojeta (1971, pl. 2, figs 1–5) refigured some of these specimens, which are all internal moulds; he remarked (1971, p. 4) that Ulrich's figures are highly interpretative, and certainly the photographs of the material show only faint impressions of the dentition. There is in all probability, therefore, little resemblance between the dentition of the two forms. In any event they differ markedly in shell shape and musculature; *Allodesma* is isomyarian, whilst *Moridunia* is markedly anisomyarian.

Moridunia simplicidens sp. nov.

Plate 5, figures 4–11

Derivation of name. From the Latin *simplex*, (= simple) and *dens*, (= tooth).

Material. 447 specimens (202 LV, 185 RV, 60 CV). Holotype: NMW 78. 17G. 161. Paratypes: NMW 78. 17G. 1–160; NMW 78. 17G. 162–447.

Diagnosis. As for genus.

Description. The holotype is an internal mould of a left valve 16.0 mm long and 12.5 mm high. The anterior adductor muscle scar is rounded and prominent with a myophoric buttress as its posterior; on its dorsal side

is a prominent triangular pedal retractor scar. The posterior adductor is far less well defined, roughly triangular, with an area over twice that of the anterior adductor. The upper (apical) region of the triangle could represent a pedal retractor scar, but there is no apparent line of separation between it and the rest of the muscle impression. The hinge-plate shows a single large prominent central pseudocardinal tooth in the left valve (Pl. 5, fig. 4); this has a smaller socket both anterior and posterior to it. The right valve (Pl. 5, fig. 8) displays well the prominent central socket in the hinge-plate corresponding to the left valve pseudocardinal tooth; in most latex casts this appears as a median gap in the right valve hinge-plate, not a socket within it, as the socket is so deep. To both the anterior and posterior of this socket is a pseudocardinal tooth; each arises from behind the hinge-plate and projects forward on it. The posterior pseudocardinal tooth is extended posteriorly so that it is parallel with and below the anterior portion of the right valve pseudolateral socket (Pl. 5, fig. 8). This tooth could thus be interpreted as the most anterior of the pseudolaterals. There is, in addition, one long posterior pseudolateral tooth in each valve. Above the right valve pseudolateral are faintly impressed ligamental nymphs, showing that the ligament was entirely opisthodontic. The pallial line is not well impressed and is not apparent on most specimens.

The shell exterior is essentially smooth; it is ornamented only by fine growth lines.

Remarks. Although *Redonia* is recorded from the upper part of the Arenig Series in Britain, (*R. anglica* occurs in the Mytton Flags of Shropshire) it appears to be absent from South Wales (although shallow water facies are not present in much of the upper Arenig there); it seems probable that *Moridunia* occupied the same ecological niche, as a shallow infaunal filter feeder, and is a major constituent (c. 35 per cent.) of the bivalve fauna at Llangynog.

There is some similarity between this species and *Modiolopsis ramseyensis* Hicks (revised by Carter (1971, p. 256, pl. 39, fig. 3) who refigured the holotype and referred it to *Actinodonta*), including the single long posterior pseudolateral tooth and the prominent anterior adductor. It is probable that the proportions of the holotype of *M. ramseyensis* (length 22.8 mm, height 10.3 mm) have been affected by the pervasive cleavage. Reasons are given above for excluding *M. ramseyensis* from *Actinodonta*, and, because of distortion of the type material and lack of preserved pseudocardinal dentition (if any), I propose to restrict Hicks' name to the type material.

Order MODIOMORPHOIDA Newell, 1969
 Superfamily MODIOMORPHOIDEA Miller, 1877
 Family MODIOLOPSIDAE Fischer, 1887
 Genus GONIOPHORA Phillips, 1848
 Subgenus COSMOGONIOPHORA McLearn, 1918

Type species. *Goniophora bellula* Billings, 1874

Goniophora (Cosmogoniophora) extensa sp. nov.

Plate 4, figures 3, 5

Derivation of name. From the extended postero-ventral margin of the valves.

Material. Seven specimens (1 LV, 2 RV, 3 CV, 1 CVE). Holotype: NMW 78. 17G. 1222. Paratypes: NMW 78. 17G. 1223–1228

Diagnosis. *Goniophora (Cosmogoniophora)* with the posterior part of the ventral margin extended.

Description. The best preserved specimen is the holotype (Pl. 4, fig. 5), a right valve 15.3 mm long and 8.7 mm high. A paratype left valve (NMW 78. 17G. 1223) is not so well preserved and appears to be slightly crushed dorso-ventrally; it is 16.3 mm long and 8.5 mm high (the latter figure probably reduced by distortion). The prosogyrate umbones are well to the anterior; from their posterior, a strong carina runs to the postero-ventral margin, fading in intensity close to the ventral margin. The postero-ventral margin is markedly extended. There are no visible muscle scars and no detail of dentition can be seen. The exterior of the shell is ornamented by

a fine radial and concentric ornament (Pl. 4, fig. 3), some elements of which appear to be visible on the internal moulds.

Remarks. The goniophorid shape and fine radial ornament indicate assignment to *Goniophora* (*Cosmogoniophora*) and the extended postero-ventral margin distinguishes this species from others, such as *G. (C.) bellula* (Billings) from the Silurian of Nova Scotia. The latter also differs in being very much larger (c. 40 mm long), but has similar ornament to *G. (C.) extensa*. The latter shows some similarity to *G. (C.)* sp. described and figured by Babin and Gutiérrez-Marco (1991, p. 123, pl. 5, figs 3–4). The Welsh form differs in being further extended at the postero-ventral angle and in having the fine radial costae over the shell surface, whilst in the Spanish examples the radial ornamentation is restricted to the area posterior to the carina.

Genus MODIOLOPSIS Hall, 1847

Type species. *Pterinea modiolaris* Conrad, 1838, by original designation (Hall 1847, p. 157).

Modiolopsis sp. A

Plate 6, figure 7

Material. Two specimens (2 CV). NMW 78. 17G 1229–1230.

Description. The more complete of the two specimens (NMW 78. 17G. 1229) is 48 mm long and c. 29 mm high. It is of elongate modioliform shape with the left valve and part of the conjoined right valve preserved. The umbones of both valves are preserved, and are small and well anterior. Beneath the umbonal area the shell is quite narrow. The width of the shell increases rapidly posteriorly right up to the gently rounded posterior margin of the valve. The anterior adductor muscle scar is small, circular and prominent; the posterior scar is considerably larger, narrow and triangular, the apex of the triangle lying anteriorly. There is no trace of any teeth and it is presumed that this species was edentulous, as moulds from this locality virtually always preserve the dentition.

Remarks. This species appears distinct from any described of this genus, but the poorly preserved material is not satisfactory for the erection of a new species. It is considerably larger than and of a different shape from *Modiolopsis homfrayi* Hicks (lectotype designated and refigured by Carter 1971). I agree with Carter (1971) that Hicks' other species of *Modiolopsis* (*M. ramseyensis* and *M. cambriensis*) are palaeoheterodonts; they may both be distorted specimens of *Moridunia*, but they are so misshapen that I recommend that their respective names should be restricted to the type material. The general shape of the specimens is close to that of *M. modiolaris* Conrad, and differs considerably from that of *M. sp. B* described below.

EXPLANATION OF PLATE 6

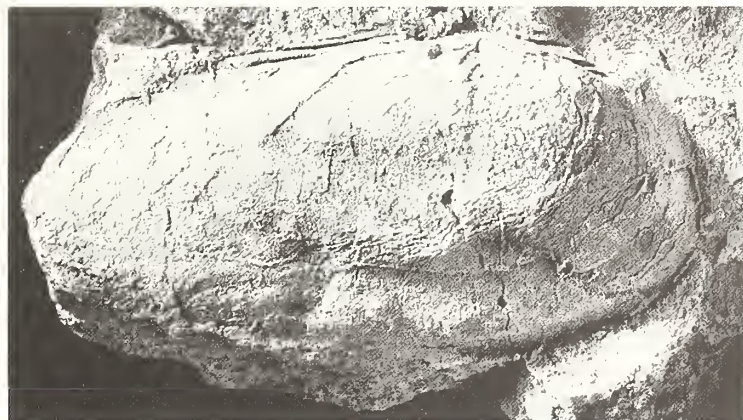
- Figs 1, 8. *Ribeiria complanata* Salter in Murchison, 1859. 1, NMW 92. 28G. 1; right valve, internal mould. 8, BGS GSM 12433, lectotype; left valve internal mould; Mytton Member, Shelve Formation, probably Whitlandian Stage, Arenig, Lord's Hill, Shelve Inlier, Shropshire; $\times 2$.
 Fig. 2. *Eurymya* sp.; NMW 78. 17G. 1239; $\times 3$.
 Figs 3–4. *Fortowensia grandis* gen. et sp. nov. 3, NMW 78. 17G. 1193; right valve, internal mould showing pallial punctae. 4, NMW 78. 17G. 1192, holotype; left valve, internal mould. Both $\times 2.8$.
 Figs 5–6. *Palaeopteria* sp.; NMW 78. 17G. 1245; latex cast and right valve internal mould; $\times 3$.
 Fig. 7. *Modiolopsis* sp. A; NMW 78. 17G. 1229; left valve which also has part of the conjoined right valve (not figured); $\times 2$.
 Fig. 9. *Cyrtodonta* cf. *wattii* (Tate, 1896); NMW 78. 17G. 1241; right valve, internal mould; $\times 2$.



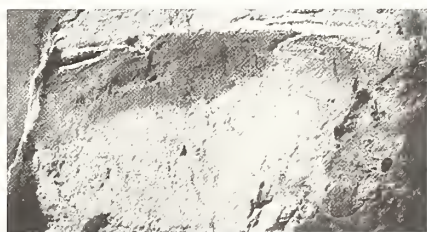
1



2



3



5



4



6



7



8



9

Modiolopsis sp. B

Plate 3, figure 7

Material. Two specimens (2 CV). NMW 78. 17G. 1231–1232.

Description. The better preserved of the specimens (NMW 78. 17G. 1231) is that figured, and is 34.2 mm long and 23.8 mm high. It has an oblique modioliform shape with its umbones placed about one-quarter of the length away from the anterior margin. The rounded anterior adductor is well impressed, but there is no obvious posterior adductor impression or any sign of teeth on either specimen. The external mould shows a shallow concentric ornament.

Remarks. The more oblique shape and shorter hinge-line of this specimen serve to distinguish it readily from *M.* sp. A. In general shape this species shows some similarities to *Dipleurodonta* Isberg, 1934 and *Eurymyella* Williams, 1912, but both of these have some teeth and it is thought that some evidence of dentition would have been preserved if *M.* sp. B originally had teeth. A generic assignment to *Modiolopsis* therefore seems preferable.

Genus PARALLELODUS Branson, 1909

Type species. *Parallelodus obliquus* Branson, 1909.

Parallelodus dyfedensis sp. nov.

Plate 5, figures 2–3

Derivation of name. From the county of Dyfed, South Wales.

Material. Four specimens (3 LV, 1 RV). Holotype: LV, NMW 78. 17G. 1233. Paratypes: NMW 78. 17G. 1234–1236.

Diagnosis. Elongate *Parallelodus*, twice as long as high, with single weak anterior and posterior lateral teeth in each valve. Shell terminated acutely postero-ventrally.

Description. The holotype is 37.8 mm long and is c. 18.5 mm high, (the ventral margin is not perfectly preserved). The internal mould is rather featureless; no muscle impressions are visible. The umbo is in the anterior third of the shell and is prosogyrate. A long blunt ridge extends back from the umbo to the acute postero-ventral angle of the shell, and although strong, is not acute enough to form a discrete carina. The left valves show the impression of a long posterior lateral tooth, arising just posterior to the umbo and running the entire length of the hinge; there is a short anterior lateral tooth which does not extend far anterior to the umbo. Although the teeth are well-defined, they are not strong features, and the corresponding sockets are shallow. The partial external moulds show that the exterior was ornamented with fine concentric growth increments, some of them occasionally stronger.

Remarks. There is good agreement in general shape with *Parallelodus obliquus*, although that species attains its maximum height about two-thirds of the way from the anterior end of the shell, whereas in *P. dyfedensis* it is nearer to the umbones. *Parallelodus* was also described by Branson (1909) as having two anterior and two posterior teeth in the right valve; one of each in the left valve. Because modiomorphoid teeth vary so considerably, dentition does not appear to be a good genus-diagnostic feature. Indeed, this variability causes problems with the placement of modiomorphoideans at subclass level. Thus, whilst Pojeta (e.g. 1978, 1987) regarded them as isofibranchs, Bailey (1983) retained them within the Palaeoheterodonta, as '*Modiomorpha*... has a heterodont arrangement with weak posterior laterals... other modiomorphids... have strong posterior elements as part of a continuous actinodont series' (Bailey 1983, p. 200). This was one of the reasons why the latter author retained the Palaeoheterodonta as a subclass. This apparent dilemma is surely

answered by regarding the modiomorphoideans as another example of a bivalve stock which is able to repeat different styles of dentition at different periods of time. In this manner the modern solemyoids can produce pseudo-actinodont dentition (Allen and Sanders 1969) as can modern nuculoids (Allen and Sanders 1973). Similarly the taxodont dentition of some neotaxodontids (see below, and Cope 1995, p. 367) does not imply any phylogenetic relationship to the palaeotaxodonts, as Cox (1959) demonstrated. I thus view the presence of teeth in the modiomorphoid stock as a feature which appears and disappears. It may help to support the hypothesis that the modiomorphoids were derived from an actinodontoid stock by loss of teeth; in this case, early Ordovician forms might well show dentition differently developed from later forms.

P. dyfedensis is also very similar in shape to the specimens of *Whiteavesia* figured by Pojeta (1971, pl. 17) although that genus is essentially edentulous. According to LaRocque and Newell (*in* Cox *et al.* 1969, p. N399) *Whiteavesia* also has an ornamentation of fine radial ridges on the interior of the shell. As the internal moulds of *P. dyfedensis* are smooth, this feature was clearly absent in these specimens.

No species of *Parallelodus* has been described hitherto from the lower Ordovician, the type species coming from the Blackriveran (middle Ordovician) of Missouri. Although there are differences in dentition and of age, neither of these appear to be major obstacles to the generic assignment made here, and a placement in *Parallelodus* is preferred, rather than to erect a new genus for a clearly closely allied form which bears fewer teeth in one valve.

Family COLPOMYIDAE Pojeta and Gilbert-Tomlinson, 1977

Remarks. This family is distinguished from the Modioloipsidae by the presence of a rather blunt 'articulation device' (Pojeta and Gilbert-Tomlinson 1977, p. 27) in the right valve, which articulates with similar or sometimes more lamellar structures in the left valve.

Genus XESTOCONCHA Pojeta and Gilbert-Tomlinson, 1977

Type species. *Xestoconcha kraciukae* Pojeta and Gilbert-Tomlinson, 1977

Xestoconcha sp.

Plate 5, figure 1

Material. Two specimens (1 LV, 1 RV). NMW 78. 17G. 1237–1238.

Description. The larger of the two specimens, left valve NMW 78. 17G. 1238 is c. 17.5 mm long (the posterior extremity is damaged) and 9.2 mm high. The right valve is 15.0 mm long and 9.2 mm high. In each case the maximum height obtains subumbonally. The umbones are prosogyrate and about two-fifths of the way from the anterior of the shell. The anterior adductor scar is moderately impressed and rounded; the posterior adductor is not visible in either specimen. There is a thick blunt tooth beneath the umbo of the left valve (Pl. 5, fig. 1) which also bears a single, rather subdued posterior blade-like tooth. The right valve may have a similar subumbonal tooth, but its preservation does not allow any posterior dentition to be seen. The external of the shell, revealed by the partial external mould, is ornamented by some fine, commarginal growth increments towards the commissural region.

Remarks. The shape of these specimens is very similar to that of the type species, figured by Pojeta and Gilbert-Tomlinson (1977, pl. 25), which is, however, slightly larger. The Welsh form also differs in the presence of the single posterior lateral tooth in the left valve. *Xestoconcha* sp. differs from *Colponya* species in having the maximum height in the anterior part of the shell (subumbonally) and in that the shell tapers posteriorly. The dentition is, however, remarkably close to that of *Colponya* species, with a single thick blunt tooth. The Welsh material shows that *Xestoconcha* has a blunt tooth in the right valve, a feature not determinable from the type species. Differences

between the Welsh and Australian material warrant specific distinction, but the preservation of the former is too poor to name it formally.

The type material of *X. kraciukae* is from the Pacoota Sandstone of the Amadeus Basin of Australia. This formation was dated as Arenig by Pojeta and Gilbert-Tomlinson (1977, pp. 3–4), and as late Tremadoc by Shergold *et al.* (1991, p. 9). Although South Wales was in a high Gondwanan latitude at this time, as opposed to the equatorial latitude of Australia, both areas are on the margins of the Gondwanan continent and bivalves which were tolerant of temperature differences could presumably have migrated larvally around the shores.

Genus EURYMYA Ulrich, 1894

Type species. Modiolopsis plana Hall, 1861.

Eurymya sp.

Plate 6, figure 2

Material. One right valve, NMW 78. 17G. 1239.

Description. The specimen is 12.0 mm long and 8.5 mm high. Maximum height is at the postero-ventral angle of the shell. The mould is rather featureless and the anterior adductor impression is shallowly impressed, virtually on the anterior margin of the shell; the posterior adductor muscle scar is not visible. There is a faintly impressed pallial line. The umbo is situated approximately one-third of the way back from the anterior end; it has been crushed downwards, thus making it difficult to determine whether there is any subumbonal dentition. There appears to be a single large blunt structure preserved beneath the umbo, but its nature cannot be ascertained without removal of the umbo which would damage the specimen. There are no anterior or posterior teeth preserved. There is an extremely fine radial striation on the posterior two-thirds of the mould which may reflect shell ornamentation, or which could be a preservational feature. There is some concentric ornament present, particularly on the post-umbonal shoulder of the shell.

Remarks. There is close correspondence in shape to the specimens of *Eurymya* figured by Pojeta (1978, particularly pl. 13, fig. 6) and Pojeta and Runnegar (1985), and also some similarity to the specimen figured by Babin and Gutiérrez-Marco (1991, pl. 5, fig. 1) as *Modiolopsis? elegantulus* Sharpe; the last appears to be more appropriately placed in *Eurymya* as far as its shape is concerned, but it is apparently edentulous. *Eurymya* was included with question in the Pterioda by Cox *et al.* (1969), but it appears to have only a single subumbonal tooth, and Pojeta (1978) decided that it was probably a modiomorphoid. Later, Pojeta and Runnegar (1985, p. 313, fig. 9) included it in the Colpomyidae.

Subclass PTERIOMORPHIA Beurlen, 1944

Order CYRTODONTIDA ord. nov.

Diagnosis. Ovoid shells with tendency to prominent prosocline umbones, with or without radial or commarginal ornamentation. Isomyarian to anisomyarian. Well-developed teeth divided into anterior group including arcuate teeth separated by edentulous area from posterior group parallel or sub-parallel to hinge margin. Ligament opisthodontic external, lamellar, duplivincular or without grooved ligament area.

Stratigraphical range. Late Tremadoc to Devonian.

Remarks. In this order, which is formed by enlarging the concept of the cyrtodontoids, I recognize two superfamilies: the Cyrtodontoidea Ulrich, 1894 and the Falcatodontoidea superfam. nov. The ligamental area of the Cyrtodontoidea bears fine longitudinal ridges and grooves, characteristic of forms with a duplivincular ligament, although as suggested by Waller (1978) these grooves may be

indicative only of an entirely lamellar ligament. The grooves and ridges intersect the dorsal margin at a very low angle, and thus more than one of these was functional at any one time (Pojeta and Runnegar 1985); it was consideration of the way that the growth lines extended onto the ligamental area which led Waller (1978) to suggest that the cyrtodontoidean ligament may have been entirely lamellar. In contrast, the ligamental area of the falcatodontoideans is devoid of grooving and the ligament was probably parivincular.

For the reasons outlined above I prefer to regard *Catamarcaia* Sánchez and Babin, 1993 as a cycloconchid with a grooved ligamental area, rather than a cyrtodontoid lacking an edentulous area on the hinge-plate.

Cope (1995) separated the superfamilies Arcoidea Lamarck, 1809 and Limopsoidea Dall, 1895 from other forms included in the order Arcoida Stoliczka, 1871 by Cox *et al.* (1969), and combined them in the subclass Neotaxodonta, Korobkov, 1954, which is characterized by a unique combination of a duplivincular ligament, a shell with crossed lamellar or complex crossed lamellar structure, and a tendency to develop taxodont dentition. The Neotaxodonta range from ?Devonian to Recent. It should be noted that Cox *et al.* (1969, p. N256) included *Glyptarca* Hicks, 1873 as a synonym of *Parallelodon*, but it is now clear that the latter is a palaeoheterodont (see above), and this removes the early Ordovician age given for the earliest *Parallelodon*. Since a new ordinal level taxon is required for the cyrtodontoids and falcatodontoids, the Cyrtodontida is established here.

Superfamily CYRTODONTOIDEA Ulrich, 1894

Family CYRTODONTIDAE Ulrich, 1894

Genus CYRTODONTA Billings, 1858

Type species. *Cyrtodonta rugosa* Billings, 1858 (by subsequent designation of Williams and Breger 1916).

Cyrtodonta cf. *staffordae* Pojeta and Gilbert-Tomlinson, 1977

Plate 5, figure 12

Material. One right valve, NMW 78. 17G. 1240.

Description. The specimen is subquadrate, but with the antero-dorsal and postero-ventral margins rounded. It is 19.4 mm long and 16.0 mm high and is strongly convex. There is a single posterior lateral tooth and a socket corresponding to a left valve tooth; no detail is visible of any anterior dentition. An ill-defined anterior circular area may be the site of the anterior adductor muscle, but there is no trace of a posterior adductor scar. The umbo scarcely projects above the dorsal line.

Remarks. There is good agreement with the holotype of *C. staffordae* in shape and general appearance; the Welsh form is, however, slightly smaller. The other point of difference is that the Australian species has a single posterior lateral tooth in the right valve, but apparently not in the left. The type material of the latter is from the Stairway Sandstone of the Amadeus Basin, which is of Llanvirn to Llandeilo age, and thus somewhat younger geologically than the specimen described here.

Cyrtodonta cf. *wattii* (Tate, 1896)

Plate 6, figure 9

Material. One right and one left valve. NMW 78. 17G. 1241–1242.

Description. The left valve is the larger specimen with an estimated length of 22 mm (the posterior extremity is broken) and is 16 mm high. The right valve is the better preserved and is figured herein. The dorsal margin is straight and the shell is obliquely elongated from the antero-dorsal to the postero-ventral margins. The adductor muscles were evidently very shallowly impressed, as no muscle scars are visible. The left valve shows one arched anterior tooth overlying a similarly arched socket and a long posterior lateral tooth. The right valve

hinge-plate is broken anteriorly, but posteriorly shows two elongated teeth and one socket. There is a slight commarginal rugation of the shell, but this is not raised strongly as in *Pharcidoconcha* Pojeta and Gilbert-Tomlinson, 1977.

Remarks. In size and shape this species shows marked similarity to *Cyrtodonta wattii* (Tate, 1896), refigured by Pojeta and Gilbert-Tomlinson (1977), from the Llanvirm-Llandeilo Stairway Sandstone of the Amadeus Basin. There is closest similarity with their plate 15, figure 2, which differs in the posterior curvature of the hinge-line. *C. wattii* also has three anterior and posterior teeth in the left valve. Although a new species may be represented by the material described above, the preservation is not good enough to name it.

Genus CYRTODONTULA Tomlin, 1931

Type species. *Whitella obliquata* Ulrich, 1890.

Cyrtodontula cf. *hadzeli* Pojeta and Gilbert-Tomlinson, 1977

Plate 4, figure 6

Material. Two specimens (LV, NMW 78. 17G. 1243; RV, NMW 78. 17G. 1244).

Description. The left valve is the more complete specimen; it is 35.0 mm long and 27.5 mm high. The dorsal line is curved anteriorly and posteriorly and shows the impressions of two anterior right valve teeth, the lower one thicker and projecting farther forwards and more strongly curved; between them is a single left valve anterior tooth. The right valve confirms this arrangement of teeth. There is an edentulous area around the umbonal region of the hinge-line, behind which is a long curved left valve posterior tooth, and above it and confined to the postero-dorsal angle is a right valve posterior tooth. The elliptical anterior adductor impression is reasonably well impressed; the posterior adductor is not visible. A subdued carina runs from the umbo towards the ventro-posterior angle, but the slight crushing of the specimen makes it difficult to determine its original strength. The partial external mould shows fine concentric ornamentation.

Remarks. There is good agreement with the description and figures of Pojeta and Gilbert-Tomlinson (1977, pl. 17, figs 8–11). The Welsh specimens are somewhat larger and have slightly different dentition, but there is closer agreement with the Australian species than, for instance with the highly tumid form figured from Spain by Babin and Gutiérrez-Marco (1991, pl. 5, figs 6–7). There appear to be no other early or mid Ordovician forms to compare with this species, but later forms, such as the late Ordovician species figured by Isberg (1934, pl. 18, figs 1–2) are also more inflated. *Sphenolium* Miller, 1889 (type species *Orthodesma cuneiforme* Miller, 1881), also from the upper Ordovician has a very similar shape, but hinge details are not known. LaRocque and Newell (*in* Cox *et al.* 1969, p. N397) included *Sphenolium* under synonymy with *Modiolopsis* with a query; however, it appears too tumid to belong to the latter, and its shape suggests cyrtodontid affinities.

Superfamily FALCATODONTOIDEA superfam. nov.

Diagnosis. Ovoid cyrtodontoids with radial ornamentation. Ligament simple, opisthodetic external.

Stratigraphical range. Known only from the lower Arenig.

Remarks. This new superfamily is based upon *Falcadonta*, described below. Its remarkable, strongly costate shell is totally different from the smooth shells of the Cyrtodontoidea. In their diagnosis of the latter, Pojeta and Gilbert-Tomlinson (1977) mention the absence of radial ornament as a characteristic feature, and this is one immediate point of distinction between the two superfamilies. The only member of the Cyrtodontoidea with ornament other than growth lines, is *Pharcidoconcha* Pojeta and Gilbert-Tomlinson, 1977 which has marked commarginal rugae.

Cyrtodontoideans are believed to have been byssate like other pteriomorphians. In view of their predominantly smooth shells it is most probable that they were infaunal; although the shell does not show obvious characters of retaining a byssus in the adult, they may well have used a weak one in much the same manner as the modern *Anadara*, as a stabilizing organ (Stanley 1972). Thus, if falcatodontoideans were byssate they would have been endobysate. Their ribbed form, on the other hand, suggests that they may have been epifaunal (epibysate), and they appear remarkably homeomorphous in external morphology with the late Palaeozoic and Mesozoic epibysate arcoids figured by Stanley (1972, fig. 15D–E). If *Falcatodonta* was epibysate (the evidence is purely on shell shape comparison), it would be the earliest epifaunal bivalve; it may be significant that although the Ambonychioidea evolved from the Cyrtodontoidea, the latter were initially infaunal, so that the Falcatodontoidea make a more attractive prospect as the origin of an often strongly ribbed, predominantly epifaunal group, although it should be noted that the ambonychians have a duplivincular ligament. At present, only the Falcatodontidae is assigned to this superfamily.

Family FALCATODONTIDAE fam. nov.

Diagnosis. As for the superfamily Falcatodontoidea.

Genus FALCATODONTA gen. nov.

Derivation of name. From the Latin *falcatus* (= sickle-shaped), referring to the shape of the anterior teeth.

Type species. *Falcatodonta costata* sp. nov.

Diagnosis. Shell with strong radial ribs and dentition of anterior curved teeth separated by edentulous area from posterior teeth which are parallel to dorsal margin of shell. Ligament external opisthodontic. Numerous accessory mantle insertion points. Integripalliate, with pallial line deeply inserted in some.

Remarks. The strongly ribbed shell is unique among early Ordovician bivalves and, apart from the ambonychids, there appears to be only one other Ordovician bivalve genus described which has strong ornamentation, *Paraphtonia* Khalfin, 1958 from the middle Ordovician of the Chu-Ili Mountains, Kazakhstan, which is believed to be a modiomorphoid (Cox *et al.* 1969, p. N398).

Stratigraphical range. Known only from the lower Arenig.

Falcatodonta costata sp. nov.

Plate 7, figures 1–11

Derivation of name. From the Latin *costatus* (= ribbed), referring to the strongly ribbed shell.

Material. 90 specimens (29 LV, 33 RV, 28 CV). Holotype: NMW 78. 17G. 975. Paratypes: NMW 78. 17G. 932–974; NMW 78. 17G. 976–1012.

Diagnosis. As for genus.

Description. The holotype is the internal mould of a right valve 12.6 mm long and 10.7 mm high. These measurements show that it is a rather squarer individual than most of the paratypes, but this specimen displays the most characteristic features of this species well and, in particular, has excellent dentition. Paratypes include smaller specimens (e.g. Pl. 7, figs 2, 5), but one, possibly gerontic individual is 18.3 mm in length.

The umbo, which is prosogyrous, is located towards the anterior end of the shell. The anterior adductor impression tends to be semicircular, with the convex side pointing towards the umbo; there is a well-marked

pedal retractor scar dorsal to the anterior adductor impression. Neither of these muscle scars is shown particularly well on the holotype, but both are well-displayed by paratype NMW 78. 17G. 976, which also shows a well impressed pallial line. The pallial line is variably impressed, but is seen on many specimens (Pl. 7). The posterior adductor is considerably larger than the anterior one, and is triangular with the acute angle of the triangle lying close to the dorsal margin of the valve.

The exterior of the shell has strong radial costae, rounded in cross section as are the equally sized intercostal areas. The ribs are crossed by growth lines which only become apparent on some of the larger shells, where there is sometimes a pronounced growth increment (e.g. Pl. 7, fig. 7). This ornament is unusual in Ordovician bivalves and recalls that seen in some Mesozoic and later species. The posterior end of the valves is flattened dorsally to produce a 'wing'.

Within the floor of the valves there is a variable number of small punctuations, which are apparent as small raised stumps on the internal mould. They are arranged in a radial fashion and tend to lie, therefore, parallel to the ribs. The best clue to the function of these punctae lies in their restriction to an area inside the pallial muscle scar (in those specimens which have a pallial line impressed; in others it is restricted to the same area of the shell), and I conclude that they represent auxilliary mantle muscle attachment sites. Similar structures were described by Newell (1942) in mytiloideans and later (1956) in Permian anomalodesmatans; they have also been reported in some lucinid heterodonts (Cox *et al.* 1969), trigonioideans (Newell and Boyd 1965), the pteriniid *Ptychopteria*, the ambonychiid *Gosseletia* and in the cyrtodont *Ptychodesma* by Bailey (1983) who referred to them as pallial punctae.

The right valve has three anterior teeth, the anterior two of which are strongly hooked forwards; the left valve also has three similarly arranged teeth. There is an edentulous area separating these anterior teeth from the posterior teeth. There are three of the latter in the right valve, two in the left. This dentition style is characteristic of cyrtodontoides.

The preservation of the external moulds of some of the conjoined specimens has allowed the preparation of latex casts which show the hinge-line well (Pl. 7, fig. 10). From these it may be inferred that *Falcatodonta* had a simple external ligament. There is certainly no sign of any grooving in the ligamental area, which would betray a duplivincular ligament, and it is suggested that the ligament in *Falcatodonta* was parivincular.

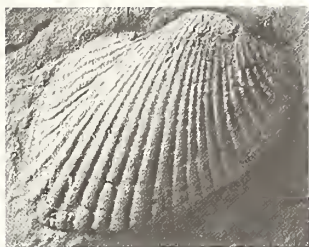
Remarks. Together with the specimens of *Cyrtodonta* and *Cyrtodontula* described above, *F. costata* is of similar age to the earliest known cyrtodontoids, *Cyrtodontula hadzeli* Pojeta and Gilbert-Tomlinson, 1977 and *Pharcidoconcha raupi* Pojeta and Gilbert-Tomlinson, 1977, both from the upper Tremadoc (see Shergold *et al.* 1991, p. 9) portion of the Pacoota Sandstone of the Amadeus Basin of Australia. Of probably similar age is *Pharcidoconcha parallela* (Hsü in Hsü and Ma, 1948) from China. The group is well known from many parts of the world by the early part of the mid Ordovician. *Falcatodonta costata* is also the only cyrtodontide yet described to lack a grooved ligamental area; in fact a duplivincular ligament usually figures in the diagnosis of the Cyrtodontoida. However, the dentition of *Falcatodonta* leaves no doubt about its taxonomic placing within the Cyrtodontida, but because of the differences in ligament type and ornament,

EXPLANATION OF PLATE 7

- Figs 1–11. *Falcatodonta costata* gen. et sp. nov. 1, NMW 78. 17G. 975, holotype; right valve, internal mould. 2, NMW 78. 17G. 976; latex cast of right valve external mould of a small individual to show ornament. 3, latex cast of holotype to show dentition and pallial punctae. 4, NMW 78. 17G. 1006; latex cast of internal mould of left valve showing dentition and pallial line. 5, internal mould of right valve as in fig. 2, to show pallial line. 6, internal mould of specimen seen in fig. 4. 7, NMW 78. 17G. 1003; latex cast of right valve, external mould showing commarginal and radial ornament; one of the very few bivalves to show abrasion. 8, NMW 78. 17G. 993; latex cast of external mould of left valve. 9, NMW 78. 17G. 986; right valve internal mould lit to show pallial punctae. 10, NMW 78. 17G. 992; latex cast of hinge region of conjoined valves. 11, NMW 78. 17G. 946; latex cast of internal mould of left valve. All $\times 3$.
- Figs 12–14. *Arenigomya carinata* gen. et sp. nov. 12, NMW 78. 17G. 1265; latex cast of external mould of left valve; $\times 3$. 13, NMW 78. 17G. 1246, holotype; internal mould of left valve; $\times 3$. 14, SEM photograph of portion of specimen in fig. 12 enlarged to show pustulose ornament; $\times 16$.



1



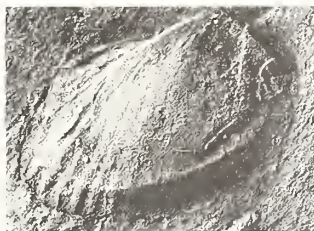
2



3



4



5



6



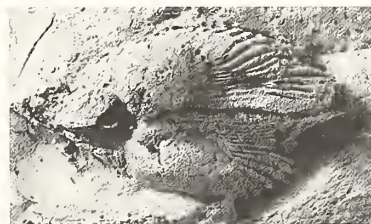
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8



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10



11



12



13



14

merits separate superfamilial status. The origins of the cyrtodontides are therefore likely to be pre-Arenig and may be sought from the glyptarcoid stock of palaeoheterodonts. These possess dentition from which a cyrtodontide type could be derived quite readily by suppression of the central teeth. Furthermore, the anterior teeth of *Glyptarca* have a configuration remarkably similar to that obtaining in many cyrtodontide genera.

The combination of the type of dentition and lack of a grooved ligamental area in the falcatodontoideans is another example of the mosaic evolution that occurred in the plexus of early Ordovician palaeoheterodonts and their descendants.

The strongly ribbed nature of *F. costata* is a distinctive character that renders it immediately identifiable. It also appears to be the earliest bivalve which has (or sometimes has) a deeply impressed pallial line.

Order PTERIOIDA Newell, 1965
Suborder PTERIINA Newell, 1965
Superfamily AMBONYCHIOIDEA Miller, 1877
Family AMBONYCHIIDAE Miller, 1877
Genus CLEIONYCHIA Ulrich, 1892

Type species. Ambonychia lamellosa Whitfield, 1882. By original designation.

Cleionychia sp.

Plate 4, figure 9

Material. A composite mould of left valve and counterpart. NMW 78. 17G. 1269.

Horizon and locality. Middle Arenig, Whitlandian Stage, from old quarry on east side of road, Llangynog, Dyfed [SN 3385 1596]; the lowest beds exposed here, on Pen-y-Moelfre Hill, have yielded a small species of *Paralenorthis* and ellesmerocerid nautiloids. *Paralenorthis proava* (Salter) and *Hesperonomiella carmelensis* Bates occur 150 m higher in the succession, a fauna also recorded from the Carmel Formation of Anglesey (Bates 1968), and there of highest Whitlandian or earliest Fennian age. The sandstones of Pen-y-Moelfre find their closest equivalents in the South Wales area with the Blaencediw Formation of the Whitland area (Fortey and Owens 1987), of early Whitlandian age.

Description. The limonite-coated composite mould is somewhat crushed and is a damaged left valve and the dorsal region of the right valve; the whole of the latter may be preserved beneath the exposed left valve. The specimen is c. 25 mm long (the posterior extremity is damaged) and is 26 mm high. The surface of the valve is ornamented by concentric growth lines; there are well-marked commarginal rugae both on the anterior and posterior parts of the valve, although these are not apparent around the middle. There is no radial ornament.

The posterior adductor muscle impression is a large rounded scar, possibly with a smaller accessory scar anterior and dorsal to this (?pedal retractor scar). Impression of the dorsal region of the right valve suggests that there may have been an anterior (pseudocardinal) tooth, almost parallel with the hinge line. In addition, the posterior extremity of the right valve shows the impression of two short ridges beneath the dorsal margin; these appear to be poorly preserved posterior teeth, but could be structures associated with the ligamental insertion.

Remarks. The strongly reduced anterior, together with the long hinge line, apparently monomyarian musculature and reduced dentition clearly identify this bivalve as an ambonychiid. Species of *Cleionychia* are very similar in lacking radial ornament, possessing rugae and having a single pseudocardinal tooth, but lack posterior lateral teeth (*vide* Newell and LaRocque in Cox *et al.* 1969) and if the Llangynog specimen does have these, a new generic assignment may be required. The earliest ambonychiids recorded are from the Chazy (= upper Llanvirn; Pojeta 1978), and this specimen predates these by a considerable margin. Because of poor preservation, this specimen is described under open nomenclature.

Superfamily PTERIOIDEA Gray, 1847

Family PTERINIIDAE Miller, 1877

Genus PALAEOPTERIA Whiteaves, 1897

Type species. Palaeopteria parvula Whiteaves, 1897 (by monotypy).

Palaeopteria sp.

Plate 6, figures 5–6

Material. One right valve, NMW 78. 17G. 1245.

Description. The specimen is 17.2 mm long and 9.2 mm high, but it appears probable that the anterior extremity of the dorsal margin is missing. The valve appears to be essentially undistorted and is moderately convex, but without the left valve it is not possible to compare the convexity of the two valves; in Whiteaves' (1897) type material both valves of *P. parvula* are convex, but the left valve more so. The hinge-line of the Llangynog example is straight and the anterior and posterior lateral teeth closely parallel the dorsal margin of the valves; there are no cardinal teeth. Two anterior and two posterior teeth are present, the latter being rather shallow; none cuts the dorsal valve margin. The posterior end of the shell is extended, but not truly auriculate. The anterior extremity of the hinge-line is missing and it is therefore not possible to judge whether there was an anterior auriculation. The umbo appears to be orthogyrate and is anterior of the centre. There is no visible impression of a posterior adductor, but there is a large scutate smooth area at the anterior extremity of the shell which could be an adductor impression.

Remarks. This specimen is kept in open nomenclature, as it is imperfectly preserved, and the left valve is unknown. The latter is considered important in a group where asymmetry of the two valves is the norm. As this is the earliest known example of a pterineid, it is quite possible, however, that the two valves were of equal convexity, since the group was presumably descended from equivalved ancestors.

Much of Whiteaves' type series consists of smaller material than the Llangynog example. He (1897, p. 182) quotes an 'average' specimen as being 5.8 mm long but also figures a much larger one, c. 15 mm long. It is clear that the Welsh specimen does not belong to *P. parvula*, as there are important differences in the ventral shape of the shell, but the straight hinge-line with its anterior and posterior laterals parallel to the dorsal margin make assignation to the Pteriniidae certain. It is believed that there are enough similarities with the Canadian material and with that figured from the Lexington Limestone of Kentucky by Pojeta (1971, pl. 11, fig. 9) to assign it to *Palaeopteria*.

This specimen of *Palaeopteria* predates the hitherto earliest known pterineid, *Denticelox turtuosa* (Tate) from the Stairway Sandstone (Llanvirn–Llandeilo) of the Amadeus Basin of Australia described by Pojeta and Gilbert-Tomlinson (1977), who also designated and refigured the lectotype. It is noteworthy that this latter species is biconvex, with the left valve showing the greater convexity.

Subclass ANOMALODESMATA Dall, 1889

Order PHOLADOMYOIDA Newell, 1965

Superfamily PHOLADOMYOIDEA Gray, 1847

Family GRAMMYSIIDAE Miller, 1877

Genus ARENIGOMYA gen. nov.

Derivation of name. Combination of Arenig with the Latin *mya* (= bivalve).

Type species. Arenigomya carinata sp. nov.

Diagnosis. Equivalve, edentulous, trapezoidal bivalve with length one-and-a-half times greater than height. Surface with fine concentric undulose ornament, radial striae and anteriorly prominent

commarginal rugae. Surface detail of finely granulose ornament. Strong carina runs from posterior side of umbo to postero-ventral margin of valves. Each valve with subumbonal articulation device.

Remarks. The oldest known anomalodesmatans described hitherto are of late mid Ordovician age (Pojeta and Runnegar 1985; Pojeta 1987); thus this record from the early Arenig extends the origin of this subclass further back into the Ordovician. Cox *et al.* (1969) listed *Davidia* Hicks, 1873 (wrongly ascribed therein to the Tremadoc rather than the Arenig) as a possible anomalodesmatan, but Carter (1971) demonstrated that the type material is uninterpretable, and refigured (1971, pl. 39, fig. 5) the type specimen of the type species (*Davidia ornata* Hicks). I have examined this specimen (BGS GSM 24197) and concur with Carter, and agree that the radiating ribs figured by Hicks (1873, pl. 5, fig. 12) and refigured by Newell (1969, fig. F3, 4) are an overoptimistic interpretation of a poorly preserved specimen. The other species of *Davidia* described by Hicks, *D. plana* (1873, pl. 5, fig. 14; Manchester Museum L10021), is also uninterpretable. Carter considered that both species could be placed in synonymy with '*Modiolopsis ramseyensis*' Hicks (which may be a redoniid palaeoheterodont), and it can be confidently concluded that *Davidia* is not an anomalodesmatan bivalve; nor is it a cycloconchid palaeoheterodont as Morris (1978) suggested (see above). The name should be restricted to that type material as Carter (1971, p. 251) recommended.

Arenigomya possesses the commarginal and beaded radial ornament with a fine scale granulose texture which is considered typical of the other Ordovician members of the group, such as *Cuneamya* Hall and Whitfield, 1875 and *Rhytimya* Ulrich, 1894, the latter overlooked by Cox *et al.* (1969). Unlike some of the other Ordovician members of this subclass, details of the hinge of *Arenigomya* are well-preserved in some specimens (Text-fig. 7). The hinge structure shows that *Arenigomya* was edentulous, but had a well-developed articulation device in each valve. Chondrophores are quite characteristic features of many Recent anomalodesmatans, but this appears to be the earliest record of a possibly analogous structure not only in the Anomalodesmata, but in any bivalve.

Stratigraphical range. Known only from the lower Arenig.

Arenigomya carinata sp. nov.

Plate 7, figures 12–14

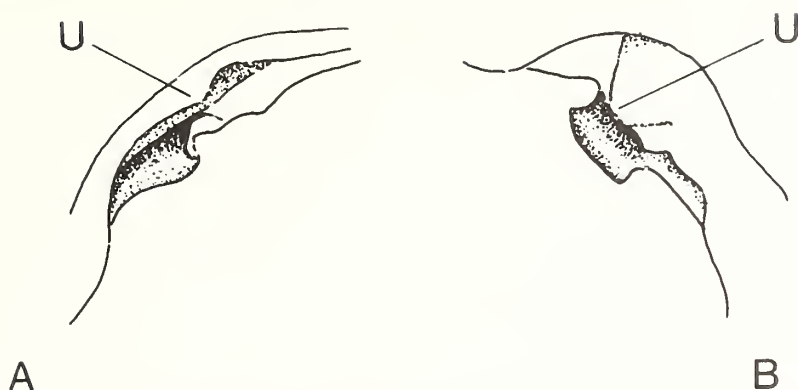
Derivation of name. From the Latin *carinata* (= carinate).

Material. 23 specimens (6 LV, 9 RV, 5 CV, 3E). Holotype: NMW 78. 17G. 1246. Paratypes: NMW 78. 17G. 1247–1268.

Diagnosis. As for genus.

Description. The holotype is a left valve composite mould 24.8 mm long with a subumbonal height of 15.5 mm. The surface is ornamented with fine radial grooves, about 4 per mm half-way down the shell; these are intersected by concentric undulose ornament of about the same spacing, giving a fine reticulate pattern. At the anterior end there is a series of strong rugae, fading posteriorly. The hinge-line is well shown by paratypes NMW 78. 17G. 1247–1248. The species is edentulous but bears a single curved plate in each valve. This is developed from the underside of the umbones (see Text-fig. 7) and is strongly concave upwards; it seems probable that this structure housed an internal ligament and can therefore be identified as a chondrophore. The well-preserved hinge area on several specimens shows that this species is edentulous.

Paratype NMW 78. 17G. 1248 shows a small, shallowly impressed anterior adductor muscle scar, but neither the posterior adductor nor the pallial line are shown by any specimens; both presumably had shallow insertion. A strong carina runs from the posterior side of the umbo to the postero-ventral margin of the valves; it



TEXT-FIG. 7. *Arenigomya carinata*; camera lucida drawings of the hinge-line of two specimens to show spoon-shaped subumbonal structures in each valve, viewed from the anterior. U = umbo. A, NMW 78. 17G. 1247; right valve. B, NMW 78. 17G. 1248; left valve. Both $\times 4$.

becomes a discrete ridge projecting for up to 1 mm above the adjacent surface of the valves. Dorsally and posteriorly to the carina the ornament is somewhat subdued.

Remarks. A carina characterizes some other Palaeozoic anomalodesmatan genera, including *Alula* Girty, 1912 (Permian) and *Sanguinolites* McCoy, 1844 (late Devonian–Permian), as well as a large number of Mesozoic and later forms; it seems to be a character of generic rather than specific distinction. The silica replacement of parts of the shell in some specimens suggests that *Arenigomya carinata* may have had a shell with a thick periostracum or high organic content of the calcareous parts of the valves, as in *Ovatoconcha*, described above.

Class ROSTROCONCHIA Pojeta, Morris and Newell, 1972

Order RIBEIRIOIDA Kobayashi, 1933

Family RIBEIRIIDAE Kobayashi, 1933

Genus RIBEIRIA Sharpe, 1853

Type species. *Ribeiria pholadiformis* Sharpe, 1853.

Ribeiria complanata Salter in Murchison, 1859

Plate 6, figures 1, 8

- 1859 *Ribeiria complanata* Salter in Murchison, p. 50, Fossils 8, fig. 3 [listed on p. 50 as *Redonia? complanata*, but corrected in Errata and Corrigenda, p. xx, to *Ribeiria*.]
- 1866 *Ribeiria complanata* Salter, p. 346, pl. 11B, fig. 16.
- 1976 *Ribeiria complanata* Salter; Pojeta and Runnegar, p. 51, pl. 9, fig. 10.

Material. NMW 92. 28G.1a–1b, internal and external moulds.

Description. The specimen has separated from the matrix exposing the right side of the crushed internal mould, but it is clear that this is of the whole of the interior of the shell. The specimen is just over 20 mm long (the posterior extremity is damaged so that the exact length is unknown) and is 9.5 mm high. There is a well-marked slit in the internal mould marking the position of the pegma. There is a possible muscle insertion point of the primary pedal retractor visible on the specimen, which is, however, rather distorted at this point (see Pojeta and Runnegar 1976, fig. 3). The dorsal margin of the mould is virtually straight and this impression is confirmed by the external mould, although the internal mould shows a raised area on the dorsum which may be a crushed impression of the posterior median muscle. As far as can be seen the posterior of the shell is rounded.

Remarks. There is reasonably good agreement between this specimen and the specimen figured by Salter and re-figured by Pojeta and Runnegar (1976, pl. 9, fig. 10) and herein (Pl. 6, fig. 8). The latter authors (p. 51) quoted their figured specimen as the holotype and only known specimen but two of Salter's specimens are in the collections of the Geological Survey (BGS GSM 12433–12434). They gave the horizon and locality of the figured specimen as 'Lower Llandeilian [*sic*], Lord's Hill, Shelve, North Wales'. This is properly the Mytton Member of the Shelve Formation, of Arenig age (probably Whitlandian Stage) of Lord's Hill, Shelve Inlier, Shropshire (Whittard 1979, pp. 16–24). Pojeta and Runnegar erroneously believed that the species dated from 1866 (Salter *in* Ramsay). In order to stabilize the nomenclature I designate BGS GSM 12434 (the figured specimen) as the lectotype. The other, rather incomplete, specimen (BGS GSM 12433) therefore becomes a paralectotype. *R. complanata* is similar to *R. pholadiformis* Sharpe from the middle Ordovician of Portugal, which is somewhat younger geologically. The main point of difference appears to be the shell thickening dorsal to the posterior pedal retractor muscle in the latter species, which produces a shallow notch in the dorsal margin of internal moulds. *R. complanata* and *R. pholadiformis* were noted by Pojeta (1979) as being two of the few species of rostroconchs to be found in clastic sediments. The Welsh specimen is a little larger than the lectotype of *R. complanata* and is somewhat crushed, but the two are clearly conspecific.

PHYLOGENY

The fauna described herein has major implications for the early radiations of the class Bivalvia, and emphasizes the key role of the western Gondwanan shelves in this (Babin 1995). Space considerations preclude a phylogenetic analysis of this fauna herein, but some of the principal conclusions have already been outlined (Cope 1995); a more thorough appraisal of the Ordovician radiation of the Bivalvia will be published elsewhere.

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NOTE ADDED IN PROOF

Since this paper was submitted, a paper by I. Hinz-Schallreuter (1995, *Muscheln (Pelecypoda) aus dem Mittelkambrium von Bornholm, Geschiebekunde aktuell*, **11**, 71–84) has been published, describing *Pojetaia* and two further palaeotaxodont genera from the Middle Cambrian of Bornholm. Amendment is thus needed to the first paragraph of this paper.

INOCERAMID LARVAL PLANKTOTROPHY: EVIDENCE FROM THE GAULT FORMATION (MIDDLE AND BASAL UPPER ALBIAN), FOLKESTONE, KENT

by R. I. KNIGHT and N. J. MORRIS

ABSTRACT. It has long been postulated that inoceramid bivalves had a long-lived planktotrophic larval stage because of their cosmopolitan distribution in the Cretaceous. This is now proven by the discovery of large larval shells preserved on inoceramid adult umbones from the Gault Formation at Folkestone. The developmental structure of these larval shells indicates that they were planktotrophic, living in the water column for in excess of 50 days. However, neither the inoceramid larval shell shape nor the hinge structure throw any new light on the taxonomic affinities of this extinct bivalve family.

INOCERAMID bivalves are very important Cretaceous biostratigraphical indices because of their cosmopolitan distribution (Dhondt 1992). It has been postulated that this distribution was due to inoceramid larvae being long-lived in the plankton (Kauffman 1975). This paper convincingly verifies these theories, for the first time, via larval shells collected during faunal analyses of the Middle and basal Upper Albian Gault Formation at Folkestone, Kent (Text-fig. 1). These specimens were found attached to squashed and fragmented inoceramid bivalve umbones, thus indicating their completion of larval ontogeny and proving their familial affinities. These adult shells were either *Birostrina concentrica* (Parkinson, 1819), *B. sulcata* (Parkinson, 1819) or *Inoceramus anglicus* Woods, 1911, the commonest inoceramids in the Gault Formation.

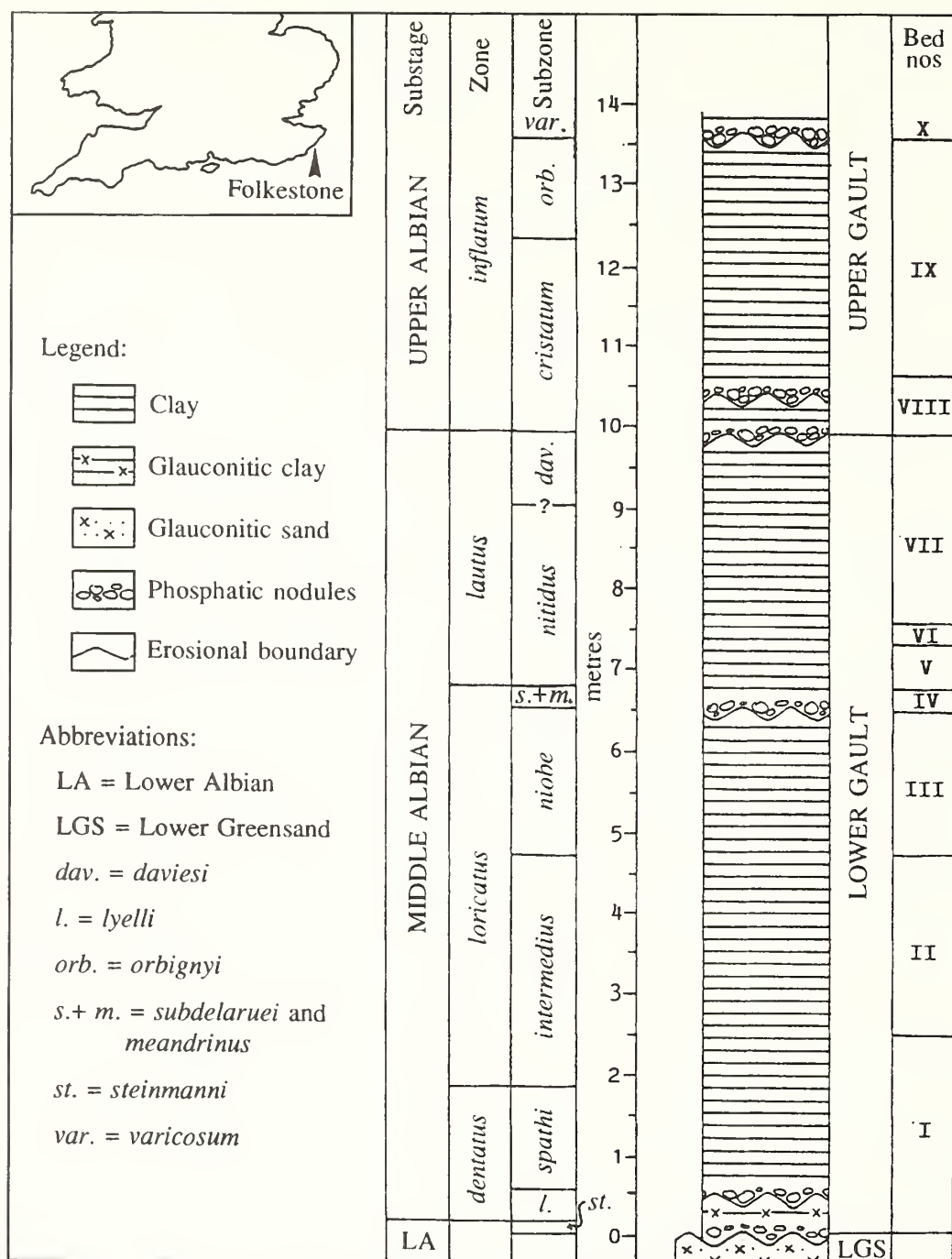
The Middle and basal Upper Albian section at Folkestone, Kent (Text-fig. 1) comprises 11 metres of highly bioturbated blue-grey clays. The section was stratigraphically divided using the lithological descriptions and biostratigraphical breakdown of Owen (1971, 1975), and within this framework specimens were collected throughout the sequence. A study of these larval shells gives an insight into aspects of the ecology of the Inoceramidae, but little indication as to the family's problematical taxonomic affinities.

The specimens have been deposited in The Natural History Museum, London.

BIVALVE LARVAL DEVELOPMENT

The classification and identification of the different developmental forms of bivalve larvae have been reviewed comprehensively by Jablonski and Lutz (1983). The majority of bivalve larvae develops from fertilized eggs via a trochophore stage, into either veligers or the test cell larva of the nuculoids. Trochophores are non-feeding (i.e. gaining sustenance from their egg) invertebrate larval stages with biconical outline, ciliated equatorial band and apical tuft (Waller 1981; Palmer 1989). The veliger is the feeding larval stage with a developing shell, through-gut and a velum used for locomotion (Erdmann 1935; Palmer 1989).

Bivalve larval shell development generally occurs in two stages. The first shell growth is called prodissoconch I (prod.I) (Werner 1939), and this develops as part of the metamorphosis from trochophore to veliger (Cox 1969). As soon as the veliger starts feeding, prodissoconch II (prod.II) is developed (Werner 1939). Prod.I, which is laid down by the shell gland, is generally micro-punctate but lacks growth lines, whilst prod. II is secreted at the mantle edge and has well-developed



TEXT-FIG. 1. Location and stratigraphy of the Gault Formation study section at Folkestone, Kent.

growth lines (Ockelmann 1965). The larvae generally develop in the water column for a period of up to about six weeks, by which time they settle to the seafloor and begin forming the adult shell, or dissoconch (Thorson 1961).

Three main development forms have been observed in modern bivalve larvae, which are identifiable by the nature of their prod.I and prod.II; planktotrophic, lecithotrophic and direct. Planktotrophy describes larval development where the veliger feeds on plankton (Thorson 1946, 1950). In these larvae, prod.I is variably developed, whilst prod.II is well-developed (Ockelmann 1965). Lecithotrophic larval development occurs via the pelagic veliger feeding on the yolk of its egg (Thorson 1946, 1950). In most lecithotrophic larvae, prod.I is either the only larval shell or an insignificant precursor to prod.II (Ockelmann 1965). Lecithotrophic and planktotrophic larval shells can be similar in terms of prod.I and prod.II. They are differentiable, however, by the number of prod.II growth lines, due to planktotrophic forms generally spending longer within the plankton.

Direct larval development also involves complete nourishment from the egg, but the larvae have no pelagic stage, developing directly to the dissoconch stage (Ockelmann 1965). This 'direct' development involves passing through the trochophore and veliger stages within the egg, which is usually protected within a brood or encapsulated system. Direct development larval shells have a large and often inflated prod.I that may exhibit irregular folds and wrinkles. Prod.II is not dissimilar to that observed in planktotrophic forms. The direct development larval bivalve shell is easily identifiable from a planktotrophic form by its ovate shape and long straight hinge-line (Ockelmann 1965).

Jablonski and Lutz (1983) suggested that there are some difficulties in using the term 'direct development' with respect to bivalve larval shell development, as it is normally only used in other organism larval systems to refer to development without a distinct intermediate veliger stage. Some workers only use the term 'direct development' with respect to bivalve larvae when this gradual differentiation into an adult occurs (Chia 1974). 'Direct development' as commonly used when describing bivalve larval growth is really a form of lecithotrophy (Sastry 1979), but without a planktonic phase.

DESCRIPTION OF THE GAULT CLAY LARVAL INOCERAMIDAE

A total of 42 inoceramid larval shells was studied; 39 from the Middle Albian and three from the Upper Albian. The well preserved Middle Albian specimens comprise 14 right valves, 11 left valves, a pair of valves and 13 of uncertain orientation. The poorly preserved Upper Albian specimens comprise two right valves and one left valve.

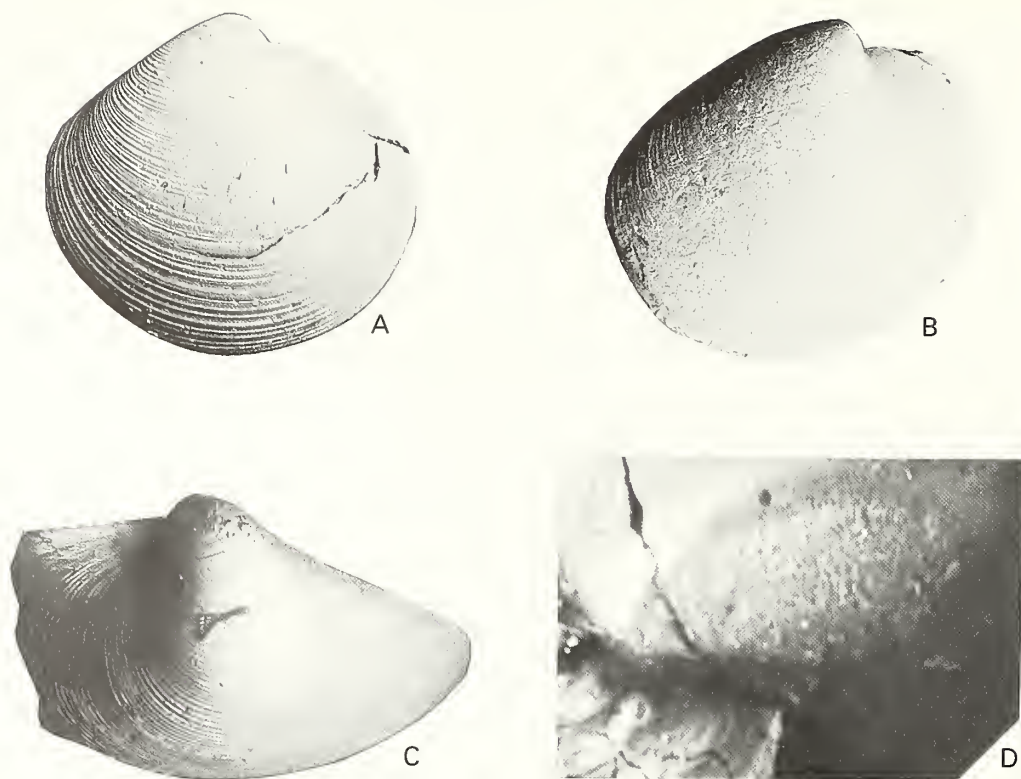
General description

The larval shells are apparently equivalve, opisthogyrous, longer than high, broader anteriorly than posteriorly, and with a prominent skewed umbo (Text-fig. 2A–C). The major part of the larval shell comprises prod.II, with prod.I being virtually imperceptible (less than 40 μm). Prod.I is micro-punctate (Text-fig. 2D), and prod.II is marked by the presence of more than 50 growth lines that appear as well-defined ridges (Text-fig. 2A, C; Pl. 1).

Size and growth lines

Gault inoceramid larval size varies from the Middle to the Upper Albian. They have a mean height and length of 1.012 mm and 1.08 mm respectively in the Middle Albian; and 0.75 mm and 0.8 mm respectively in the Upper Albian. These size variations occur in larval shells that have similar numbers of growth lines, though are probably not found on the same inoceramid species. The Middle Albian specimens are either *Birostrina concentrica* or *Inoceramus anglicus* larvae, whilst the Upper Albian specimens are probably *B. sulcata*.

The 50 or so distinct growth lines on prod.II of Gault inoceramid larvae (Text-fig. 2A; Pl. 1) are not spaced uniformly across the shell. Instead, constrictions of growth can be observed with



TEXT-FIG. 2. Shape of inoceramid larval shells from Bed II of the Gault Formation, Folkestone; *intermedius* Subzone. A–B, LL41641, left valve. A, $\times 45$; B, $\times 65$. C, LL41639, dorsal view of the right valve, $\times 100$. D, LL41641, prodissococonch II, $\times 725$.

uniformly spaced growth lines packaged between. The number of growth lines sandwiched between constrictions is variable both between and within specimens. No obvious pattern can be discerned. Only the final growth increment has relatively constant numbers of well-spaced growth lines (6–9) in all specimens (Text-fig. 2A; Pl. 1).

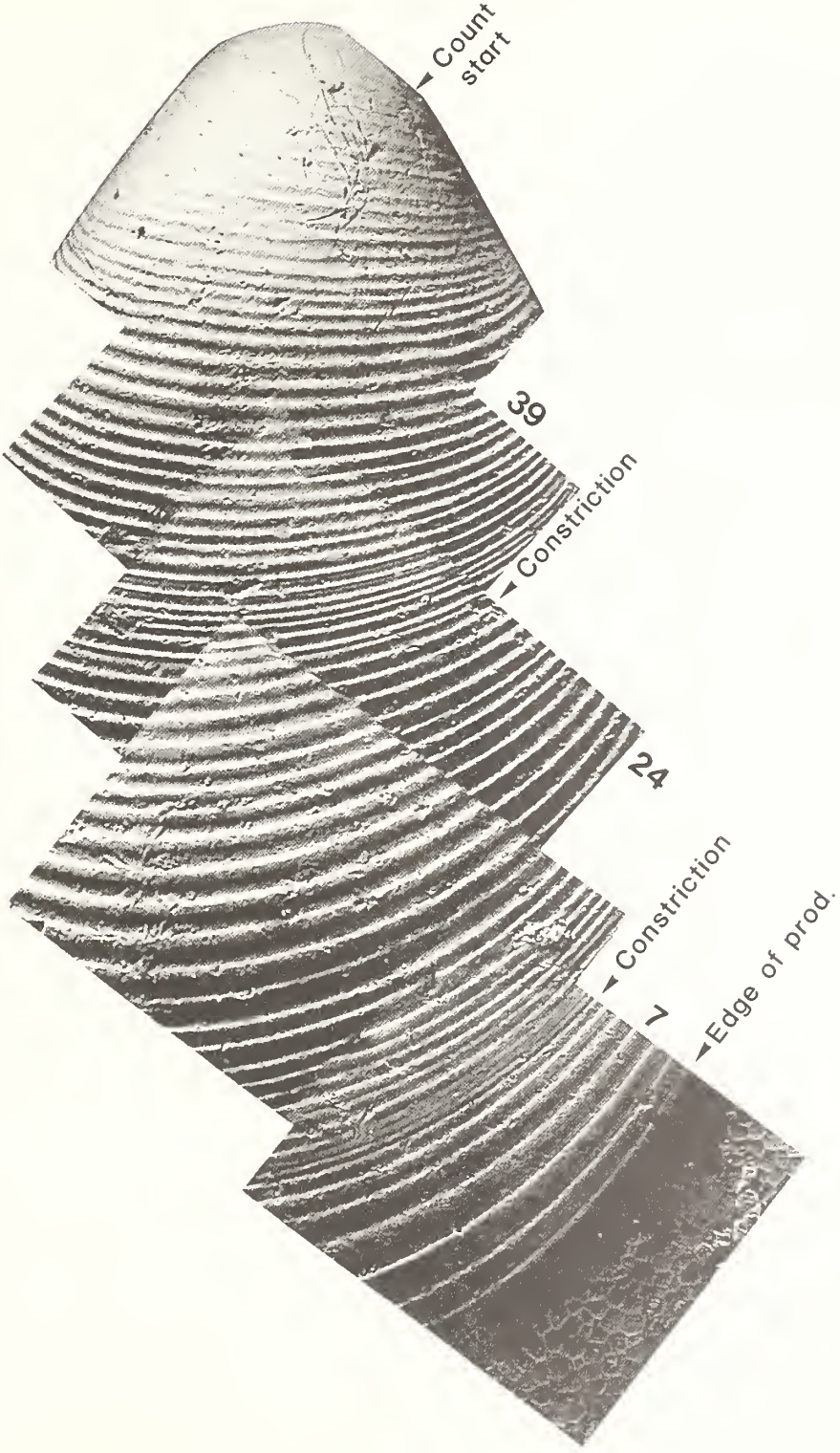
The inoceramid larvae were therefore at least twice as big as most modern and ancient larvae, and had substantially more growth lines (LaBarbera 1974; Waller 1981; Tanabe and Zushi 1988; Palmer 1989; Malchus 1995).

Muscle scars

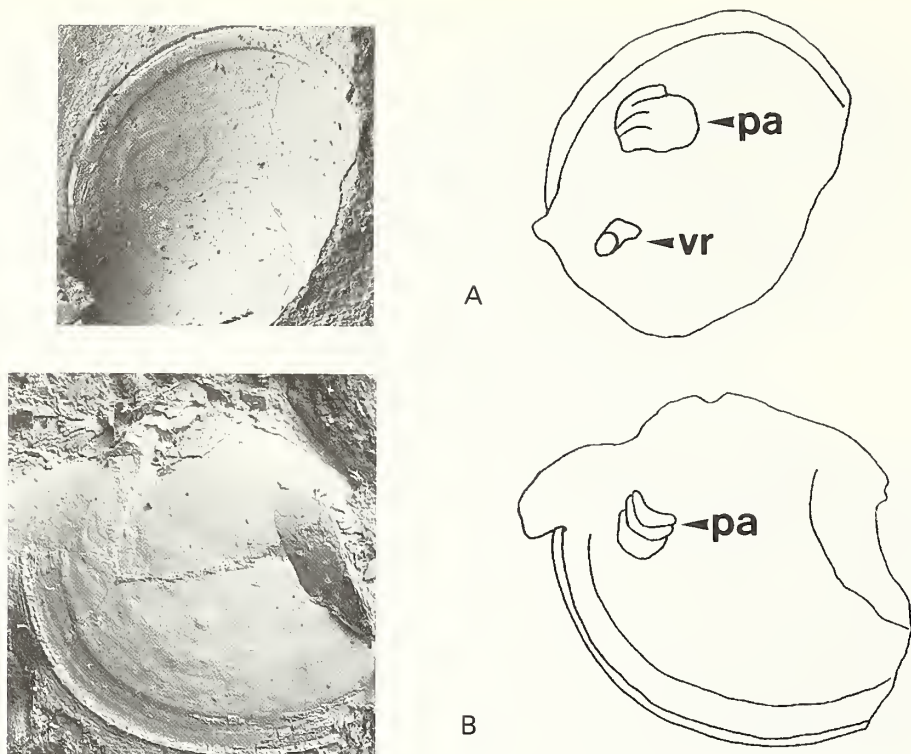
In two specimens, muscle scars can be observed. Two scars appear to be attachment areas of posterior adductor muscles (Text-fig. 3A–B). A third muscle scar, which is subovate and smaller than the adductor, is situated towards the umbo (Text-fig. 3A). This is in the position postulated for a velar retractor muscle scar.

EXPLANATION OF PLATE 1

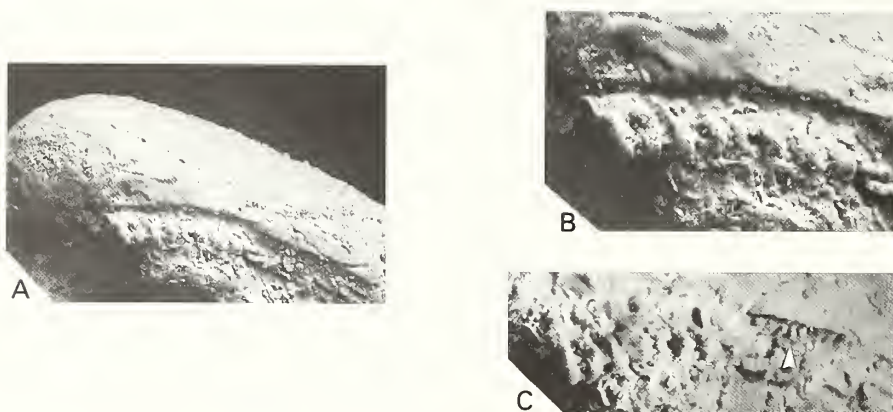
Composite of an inoceramid larval shell (LL41639) from the Gault Formation, Folkestone, showing growth line organization. Numbers indicate growth line counts between constrictions; $\times 27$.



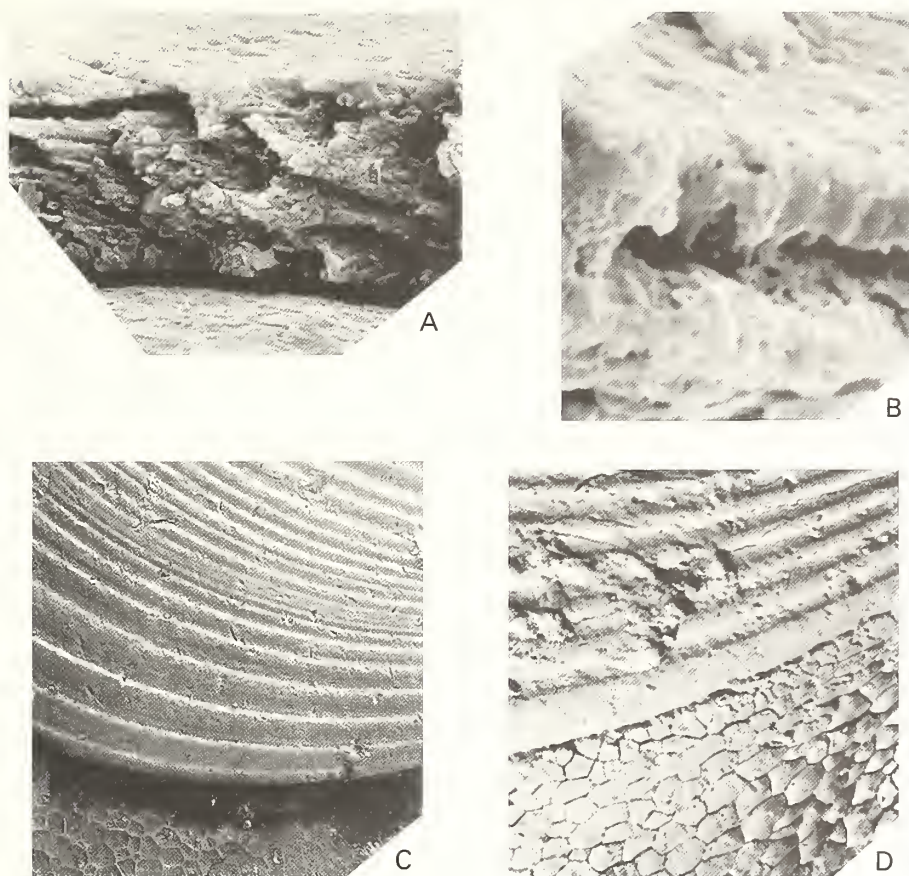
KNIGHT and MORRIS, inoceramid larval shell



TEXT-FIG. 3. Inoceramid larval musculature. A, LL41644, inner surface of an inoceramid larval shell showing incrementally developed posterior adductor (pa) and velar retractor (vr) muscle scars; $\times 28$. B, LL41643, internal mould of an inoceramid larval shell showing incrementally developed posterior adductor (pa) muscle scar; $\times 50$. Both from Bed V, *nitidus* Subzone, Gault Formation, Folkestone.



TEXT-FIG. 4. Inoceramid larval hinge structure. A-C, LL41640, inoceramid larval anterior hinge dentition of the left valve, Bed VIII(iii), *cristatum* Subzone, Gault Formation, Folkestone. A, overall view of the dentition, $\times 190$. B, provincular teeth, $\times 350$. C, denticles within the antero-dorsal groove (marked by the arrow), $\times 350$.



TEXT-FIG. 5. Inoceramid larval ultrastructure. A–B, LL41639. A, distally sloping inclined sheets of larval aragonite overlying nacreous dissoconch, $\times 4000$. B, prodissoconch outer surface aragonitic prisms, $\times 8000$. C–D, relationship between the prodissoconch and the outer prismatic calcite of the dissoconch. C, LL41639, $\times 225$. D, LL41649, $\times 300$. All from Bed I/II, *intermedius* Subzone; Gault Formation, Folkestone.

The posterior adductor scars appear to have formed by incremental growth. They exhibit distinct bandings parallel to their ventral margin (Text-fig. 3A–B), apparently related to constrictive growth periods. The maximum number of muscle growth bands found is three, which matches the number of different growth phases in prod. II of specimen LL41639 (Pl. 1).

Hinge definition

In our specimens, only the anterior hinge dentition is preserved, and then only in poor condition. The larval shells have numerous rectangular, 'taxodont'-like provincular teeth with rounded apices that are equal in size (Text-fig. 4A–B). They are evenly projecting and regularly arranged on a raised ridge parallel to the antero-dorsal margin. They are separated from the dorsal margin by a narrow groove (Text-fig. 4B).

Distal to the provincular teeth and within the groove, close to the antero-dorsal margin, there is a series of at least ten very much smaller denticles (Text-fig. 4C). The position of the ligament attachment cannot be ascertained from the specimens studied.

Larval shell ultrastructure

The ultrastructure of Gault inoceramid larval shells may be observed only in well-preserved specimens. In common with all known Recent bivalve larvae, the calcium carbonate component appears to be aragonite. It is characterized by inclined sheets that slope distally, and appears to be made up of smaller needle-like components (Text-fig. 5A–B). This is reminiscent of aragonitic crossed-lamellar ultrastructure of adult extant bivalves (Taylor *et al.* 1969; Carter 1990). The outer surface ultrastructure of the inoceramid larval shell is made up of aragonitic prisms (Text-fig. 5B). Similarly inclined and prismatic aragonitic ultrastructure is observed in prod. II of *Ostrea edulis* (Waller 1981, p. 60, fig. 147), although the inner aragonite prismatic layer of the oyster has not been found in inoceramid prod. II. The larval shell ultrastructure also appears to be highly porous, as if it was initially packed with organic material (Text-fig. 5A).

The majority of the inner surface of the inoceramid larval shell is underlain by the nacre of the dissoconch (Text-fig. 5A). The adult outer calcite prisms only occur below the periphery of prod. II (Text-fig. 5C–D). The same arrangement of prodissoconch and dissoconch is observed in the Ostreidae (Waller 1981).

DISCUSSION

Inoceramid larval palaeoecology

The Gault inoceramid larvae have features reminiscent of planktotrophic and lecithotrophic forms. The small size of prod. I (Text-fig. 2D) indicates that the original gametes were fertilized in the water (i.e. oviparous; Ockelmann 1965), and the numerous growth lines in prod. II (Text-fig. 2A; Pl. 1) indicate that they were planktotrophic. They probably spent in excess of 50 days in the plankton, given that one growth line in modern bivalve larvae is usually constructed in one day (Millar 1968). This now proven long-lived planktotrophic larval life-mode explains the cosmopolitan distribution of the Inoceramidae during the Cretaceous. In modern oceans, larvae remaining in the plankton for 50–60 days could be transported up to 150 and 500 km by a current of only 0.5 km/h (Schetema 1977). The Cretaceous marine realm included far more extensive shallow epicontinental seas than today because of the lack of polar ice caps. These were perfect areas for colonization and further distribution of the Inoceramidae.

Bivalve growth line organization, both larval and adult, has been linked to environmental (Baker 1964) and endogenous/genetic (Millar 1968) factors. The consistent number of growth lines observed on inoceramid larval specimens indicates a genetic control, whereas the random nature of the constrictions implies environmental factors. This suggests that inoceramid larval growth was mainly genetically controlled, but was sometimes modified by environmental factors (Millar 1968). The settling of the inoceramid larval shell was therefore also genetically controlled, with the final prod. II growth increment (Text-fig. 2A; Pl. 1) representing the first stage of pediveliger development (Bayne 1965). The continued larval shell growth suggests normal feeding, with the gradual starvation that is associated with pediveliger metamorphosis being recorded by non-growth.

The growth rate of bivalve larvae is affected by water temperature, with larger prodissoconchs of a given species occurring in cold water (Lutz and Jablonski 1978b). There is a decrease in inoceramid larval size between the Middle and basal Upper Albian, that could be attributed to increasing surface water temperature and climatic warming. However, the inoceramid larval shell size variability may be genetically controlled, as generic and specific classification of the specimens is problematical.

Inoceramid taxonomic affinities

The opisthocyrt veneriform shape of the inoceramid prodissoconch (Text-fig. 2A–B) resembles that of the Jurassic Gryphaeidae (Palmer 1989) and Recent Crassostrea (Chanley and Andrews 1971). The inoceramid larval hinge structure (Text-fig. 4A–C) resembles that of the Arcacea, Veneracea, Mactracea and Tellinacea (Rees 1950), as well as the Pinnidae (Booth 1979). However, though these

morphological characters have been used previously to identify fossil bivalve larvae (Lutz and Jablonski 1978a), they are now recognized as being poor diagnostic characters for identification (Chanley and Andrews 1971; Lutz and Jablonski 1981). Therefore, the inoceramid larval characteristics described in this paper throw little light on the problem of the taxonomic affinities of the extinct Inoceramidae.

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PROBLEMATICAL FOSSIL CNIDARIANS FROM THE UPPER ORDOVICIAN OF THE NORTH-CENTRAL USA

by HEYO VAN ITEN, JULIE ANN FITZKE and ROBT S. COX

ABSTRACT. *Sphenothallus* sp. and eight species of conulariids, distributed among the genera *Climacoconus*, *Conularia*, *Glyptoconularia* and *Metacoconularia*, occur in the Elgin Member of the Maquoketa Formation (upper Ordovician) of north-eastern Iowa and south-eastern Minnesota, USA. Seven of the eight conulariid species exhibit internal test structures at their corners and/or midlines. Comparisons of these test structures with internal thecal structures of coronatid scyphozoans corroborate the hypothesis that conulariids were more closely related to scyphozoan cnidarians than they were to any other extant taxon of comparable rank. *Sphenothallus* and conulariids occur in all four Elgin Member biofacies. However, the distribution of *Climacoconus* and *Conularia* is facies-dependent, with *Climacoconus* occurring predominantly in the brachiopod-echinoderm biofacies and the basal Maquoketa phosphorite, *Conularia splendida* predominantly in the trilobite-dominated biofacies, and *C. trentonensis* predominantly in the brachiopod-echinoderm, mixed faunas and graptolite shales biofacies. Conulariids commonly occur in monospecific clusters, possibly clonal in origin, and some specimens show orientational evidence of original attachment to *Sphenothallus* or nautiloid shell material. Together with previously reported data on the distribution and biostratigraphy of *Sphenothallus* and conulariids, these results suggest that both taxa were sessile benthic organisms that inhabited all major Elgin Member bottom environments, including a shallow, oxic carbonate shelf and a deeper, dysoxic shelf margin and shale basin slope. One new species, *Climacoconus sinclairi*, is described.

CONULARIIDS and their possible close relative *Sphenothallus* Hall, 1847 are widely distributed in Palaeozoic marine strata and are often mutually associated. Both may occur in exceptional abundance in certain rock units. Among the best known units previously discussed are the middle Ordovician Šárka and Dobrotivá formations of Bohemia (conulariids; e.g. Havlíček 1966), the upper Ordovician May Sandstone of Brittany (conulariids; e.g. Bouček 1928) and the upper Ordovician Collingwood Formation of Ontario and Quebec (conulariids and *Sphenothallus*; e.g. Bolton 1994). *Sphenothallus* and conulariids often occur in dark shales and lime mudstones in which normal marine taxa such as echinoderms and articulate brachiopods are rare or absent. Together with evidence suggesting that *Sphenothallus* and conulariids were sessile benthic organisms (e.g. Bodenbender *et al.* 1989; Van Iten 1991b), such occurrences raise the possibility that these taxa were capable of living in bottom waters subject to oxygen depletion and/or other forms of stress.

Recent analyses of large numbers of *Sphenothallus* and conulariid specimens from deposits such as those mentioned above have substantially increased our knowledge of anatomical variation within these organisms, and have provided evidence bearing on alternative interpretations of their mode of life and life history (e.g. Bodenbender *et al.* 1989; Van Iten 1991c, 1992a; Van Iten *et al.* 1992; Jerre 1993, 1994). This work has also contributed to discussions of the phylogenetic affinities of these taxa, one or both of which have been variously interpreted as annelids or other 'worms' (*Sphenothallus* and conulariids; e.g. Clarke 1913; Moore *et al.* 1952; Mason and Yochelson 1985; Fauchald *et al.* 1986; Babcock 1991), hemichordates or chordates (conulariids; Termier and Termier 1949, 1953; Steul 1984), an independent phylum (conulariids; e.g. Kozłowski 1968; Babcock and Feldmann 1986a; Babcock 1990, 1991; Yochelson 1991) or close relatives of hydrozoan or scyphozoan cnidarians (*Sphenothallus* and conulariids; e.g. Price 1920; Kiderlen

1937; Moore and Harrington 1956; Chapman 1966; Werner 1966, 1967; Glaessner 1971, 1984; Bischoff 1978; Grasshoff 1984; Van Iten 1991a, 1992a, 1992b, 1992c; Van Iten and Cox 1992; Van Iten *et al.* 1992; Jerre 1994).

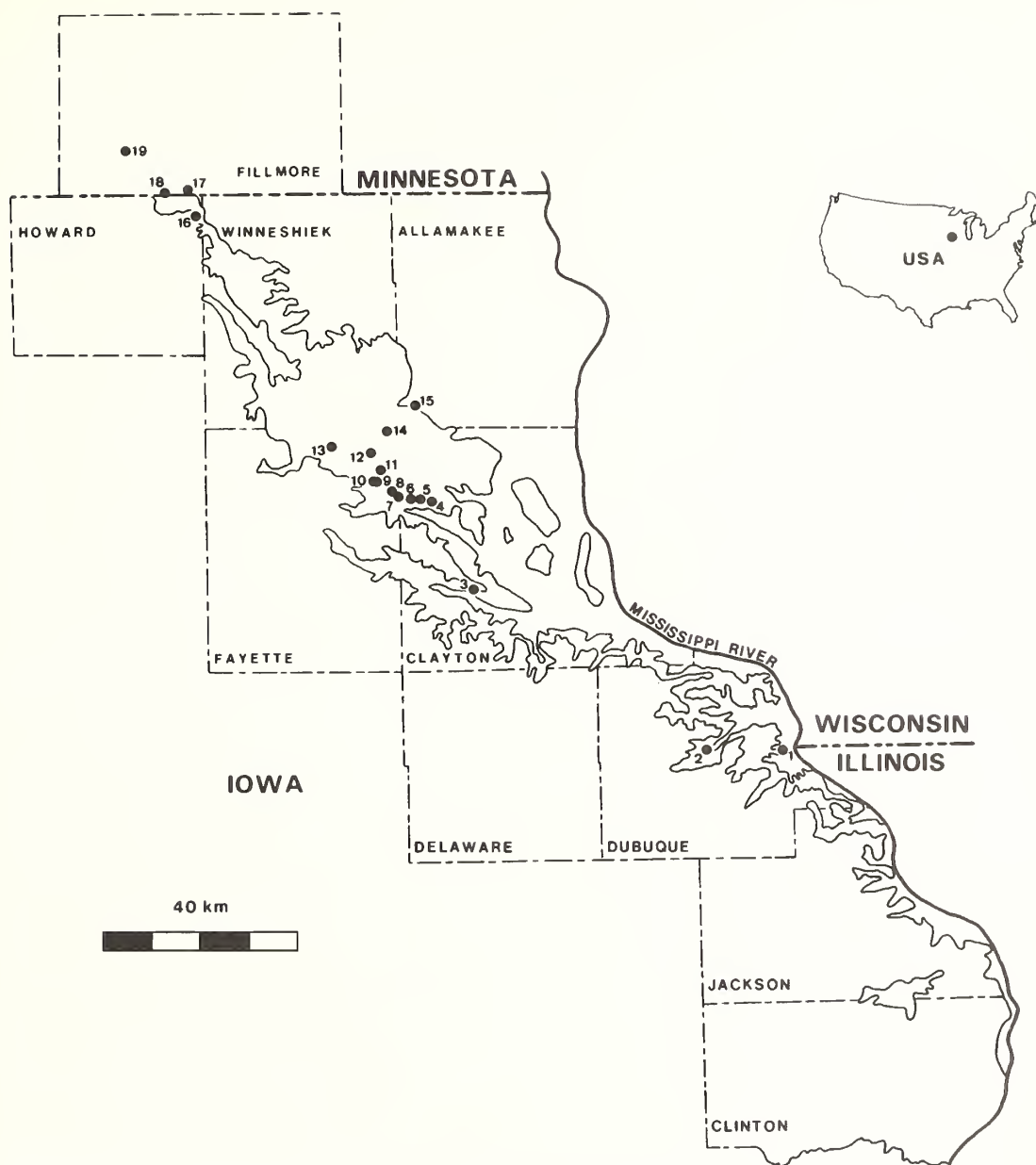
The present paper addresses the taxonomy and palaeoecology of *Sphenothallus* and conulariids in the Elgin Member of the Maquoketa Formation (upper Ordovician) of north-eastern Iowa and south-eastern Minnesota, USA. The purpose of this study is to document the exceptionally diverse Elgin *Sphenothallus*/conulariid fauna and to interpret aspects of the anatomy and distribution of these taxa having an important bearing on discussions of their affinities and palaeoecology. The Maysvillian (late Caradoc) Elgin Member has long been known for its abundant trilobites, echinoderms, brachiopods and molluscs (e.g. Slocum 1914; Slocum and Foerste 1920; Walter 1924; Ladd 1929; Miller and Youngquist 1949; Tasch 1955; Bretsky and Bermingham 1970; Whittington 1971). Until now, however, this unit had not been recognized as a major *Sphenothallus*/conulariid horizon. The Elgin Member contains eight species of conulariids representing the genera *Climacoconus* Sinclair, *Conularia* Miller in Sowerby, *Glyptoconularia* Sinclair and *Metaconularia* Foerste. One species is new. With the possible exceptions of the middle Ordovician Trenton Group of New York and Quebec and the lower Silurian Manitoulin Dolomite of northern Michigan and south-western Ontario (Sinclair 1948), no other North American stratigraphical unit contains as many conulariid genera and species as does the Elgin Member.

The Elgin Member consists of intertonguing shales and carbonates deposited in a density-stratified epeiric sea the bottom waters of which were dysoxic or anoxic over large areas (Witzke 1980, 1987; Witzke and Kolata 1989). Coupled with the unusually high diversity and abundance of Elgin *Sphenothallus* and conulariids, the substantial facies variation of this unit makes it an attractive setting for the analysis of the palaeoecology of these two groups. In particular, conulariids have been variously interpreted as sessile benthic (e.g. Babcock *et al.* 1987a, 1987b; Van Iten 1991a, 1991b), nektonic (e.g. Havlíček 1966) or planktonic or pseudoplanktonic organisms (e.g. Ruedemann 1934; Babcock and Feldmann 1984, 1986b). As will be discussed below, conulariids occur in all Elgin facies, but the distribution of conulariid species is facies-dependent. Moreover, conulariid specimens may occur in undisturbed life clusters or preserve orientational evidence of primary apical attachment to nautiloid shells and *Sphenothallus* tubules.

MATERIALS AND METHODS

The present study is based on direct examination of specimens collected from over 20 localities in the northern and central parts of the Maquoketa outcrop belt of north-eastern Iowa and south-eastern Minnesota (Text-fig. 1; Appendix 1). The sample consists of approximately 350 macroscopic specimens, mostly conulariids, and minute (about 1 to 2 mm long) conulariid and *Sphenothallus* test fragments (e.g. Pl. 2, fig. 2) obtained by dissolving pieces of limestone approximately 1 kg in mass in 4N formic acid. Test fragments were picked from undissolved residues washed on a 63 μ m brass screen. The limestone samples (Appendix 2) were collected in place, at 1 m intervals, from localities (4, 8, 16–17 and 19) that together expose most of the currently recognized stratigraphical units within the carbonate portion of the member. Test fragment samples are housed in the Department of Geology, State University of Iowa, under collection number 84492.

Abbreviations of North American institutions housing specimens examined in this study are as follows: AC, Augustana College, Rock Island, Illinois; AMNH, American Museum of Natural History, New York; CCPC, Department of Geology, Carleton College, Northfield, Minnesota; FMNH, Field Museum of Natural History, Chicago; GSC, Geological Survey of Canada, Ottawa; NYSM, New York State Museum, Albany; SU1, State University of Iowa, Iowa City; UMMP, University of Michigan Museum of Paleontology, Ann Arbor; U MPC, University of Minnesota Paleontology Collections, Minneapolis; WSU, Winona State University, Winona, Minnesota.



TEXT-FIG. 1. Map of the Maquoketa Formation/Elgin Member (upper Ordovician) outcrop belt in north-eastern Iowa and south-eastern Minnesota, USA. Numbered dots represent collecting localities that yielded *Sphenothallus* and/or conulariid specimens examined in the present study (see Appendix 1).

STRATIGRAPHY AND DEPOSITIONAL ENVIRONMENTS

Maquoketa Formation

The Maquoketa Formation (considered to be a group by stratigraphers in Illinois, Indiana and Wisconsin; e.g. Gray 1972; Sison 1980; Kolata and Graese 1983) ranges from Maysvillian to Richmondian (Caradoc to Ashgill) and underlies much of the north-central United States east of

the Transcontinental Arch (Witzke 1980, 1987; Witzke and Kolata 1989). The formation consists of two major facies: cherty shelf carbonates, preserved mainly in the subsurface and extending from eastern Iowa to the Transcontinental Arch; and shale-dominated strata developed east and south of this region, primarily in south-eastern Wisconsin, Illinois, Indiana, north-eastern Missouri and eastern Iowa. Shale-dominated strata occur at the surface primarily in south-eastern Wisconsin, western Illinois, north-eastern Missouri, south-eastern Minnesota and north-eastern Iowa. In north-eastern Iowa and south-eastern Minnesota, these beds range from about 30 to 100 m thick and crop out sporadically in a narrow, north-west–south-east-trending belt that extends from north-eastern Clinton County, Iowa to southern Fillmore County, Minnesota (Parker *et al.* 1959; Parker 1971; Text-fig. 1). In most of the north-western half of the outcrop belt the Maquoketa Formation consists of five members. Listed in ascending order, these are the Elgin Shaly Limestone, the Clermont Shale, the Fort Atkinson Limestone, the Brainard Shale and the Neda Shale. Due in part to pre-mid Devonian erosion, only the Elgin Member is present in Minnesota. South of a line extending through southernmost Clayton and Fayette counties, Iowa, the Elgin Member consists mainly of dark shales, and the rest of the Maquoketa Formation is composed almost entirely of lighter-coloured shales assigned to the Brainard Member. In both north-eastern Iowa and south-eastern Minnesota, the Maquoketa (Elgin Member) rests conformably on shaly limestones of the upper Ordovician Dubuque Formation, while the top of the formation is marked by an unconformity overlain by lower Silurian dolostones (north-eastern Iowa) or middle Devonian limestones (south-eastern Minnesota).

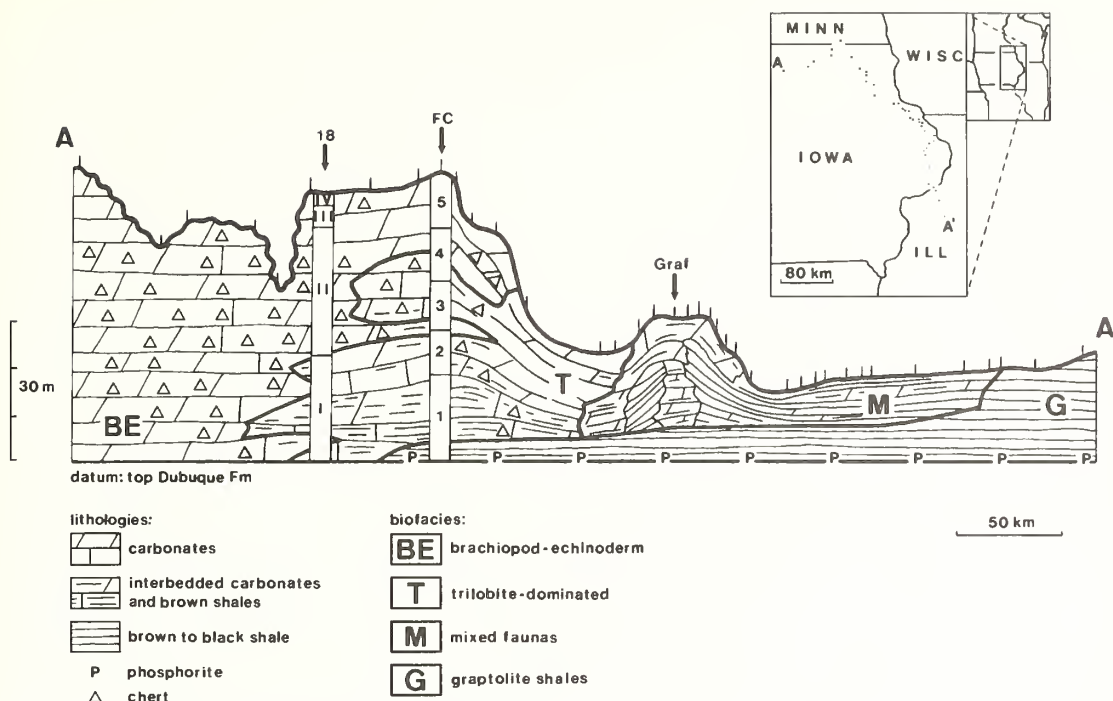
Elgin Member

The Elgin Member in the Iowa/Minnesota outcrop belt represents a shallowing-upward sequence showing maximum facies variation along a north-west–south-east transect (Witzke 1980, 1987; Text-fig. 2). Except in Minnesota, where Maquoketa strata have been deeply eroded, the Elgin Member is conformably overlain by shales of the Clermont or Brainard members. In the Iowa/Minnesota border area, in southernmost Fillmore County, Minnesota and the northernmost parts of Howard and Winneshiek Counties, Iowa, the Elgin consists predominantly of grey and light grey biomicrites and has been subdivided into four subunits, designated Lithosomes I–IV (Bayer 1967; Elias *et al.* 1988; Text-fig. 2). Lithosome I is characterized by a sparse, low diversity macrofauna dominated by graptolites and the trilobite *Isotelus iowensis* Owen. Lithosomes II and III are cherty and contain abundant, diverse invertebrate faunas including articulate brachiopods, pelecypods, nautiloids, trilobites, crinoids, sponges and solitary rugose corals.

South of the Iowa/Minnesota border area, in a region encompassing parts of south-eastern Winneshiek, south-western Allamakee, north-eastern Fayette and north-western Clayton counties, Iowa, the Elgin Member consists predominantly of thin biomicrites interbedded with brown graptolitic shales. Elgin Member strata can be subdivided over much of this area into five units, designated Units 1–5 (Parker *et al.* 1959; Text-fig. 2). Unit 1 is separated from the underlying Dubuque Formation by a thin phosphate horizon, the basal Maquoketa phosphorite, that occurs at the base of the Elgin Member throughout most of north-eastern Iowa. Units 1–3 are similar palaeontologically to Lithosome I, while Units 4 and 5 contain diverse macrofaunas consisting of abundant trilobites as well as articulate brachiopods, nautiloids, gastropods, crinoids, cystoids and sponges.

In the southern part of the Maquoketa outcrop belt, in south-eastern Fayette, southern Clayton and eastern Dubuque, Jackson and Clinton counties, Iowa, the Elgin Member consists mostly of brown to grey or black, graptolitic shales with locally abundant inarticulate brachiopods (*Lingula*) and rare trilobites (Text-fig. 2). In the vicinity of the village of Graf, north-eastern Dubuque County, the upper part of the unit exhibits numerous thin interbeds of dolostone containing abundant nautiloids and rare crinoids and bryozoans.

The lithological units described above together define four mutually intertonguing biofacies (Witzke 1980, 1987; Text-fig. 2). Moving from north-west to south-east, these are (1) the brachiopod-echinoderm biofacies (Lithosomes II and III of Bayer 1967; Units 4 and 5 of Parker *et*



TEXT-FIG. 2. North-west-south-east stratigraphical cross section of the Elgin Member of the Maquoketa Formation (upper Ordovician) in north-eastern Iowa and south-eastern Minnesota, USA. Stratigraphical column labelled 'FC' represents the Fitzgerald Creek measured section of Parker *et al.* (1959, fig. 2b); stratigraphical column labelled '18' (Locality 18) represents the measured section of Bayer (1967, fig. 2). Text-figure modified from Witzke (1987, fig. 4).

al. 1959); (2) the trilobite-dominated biofacies (Lithosome I of Bayer 1967; Units 1–3 of Parker *et al.* 1959); (3) the mixed faunas biofacies (alternating brown to black graptolitic shales and phosphatic dolomites); and (4) the graptolite shales biofacies (brown to black graptolitic shales stratigraphically below and lateral to the mixed faunas beds). These four biofacies were originally deposited in 'contrasting water masses of a stratified epicontinental seaway' (Witzke 1987, p. 239), in 'three general bathymetric settings: (1) shallow carbonate shelf [brachiopod-echinoderm biofacies]; (2) shelf margin (deepening to the southeast) [trilobite-dominated and mixed faunas biofacies]; and (3) basin slope [graptolite shales biofacies]' (Witzke 1987, p. 237). The shallow carbonate shelf, represented by Lithosomes II and III and Units 4 and 5, was deposited in areas where a well-mixed, oxic upper water mass impinged on the sea floor. Deposition here was generally below fair-weather wave base but above storm wave base (Elias *et al.* 1988). On more proximal parts of the shallow carbonate shelf, sandy lime muds lacking benthic organisms (Lithosome IV) were deposited in waters that were highly restricted. Below the oxic upper water mass, in the proximal shelf slope environment, asaphid-graptolite mudstones of the trilobite-dominated biofacies were deposited in the upper part of a zone of increasing density and decreasing oxygen content, or pycnocline. Deposition of the grey to dark grey, pyritic asaphid-graptolite mudstones of Unit I and Lithosome I probably occurred in dysoxic waters. The distal shelf slope, largely deposited in lower pycnoclinal waters that were further depleted in oxygen, was the site of graptolitic shale sedimentation (lowermost mixed faunas facies and brown to grey organic shales of the graptolite shales biofacies). Below the pycnocline, deposition of grey to black laminated shales commonly lacking benthic invertebrates (parts of the graptolite shales biofacies) took place at the base of a relatively deep water mass that was dysoxic to anoxic.

Based on these interpretations of depositional environments and on inspection of exposures showing transitions between facies, we propose the following chronostratigraphical correlations of Elgin Member subunits. As suggested by Witzke (1980), the basal Maquoketa phosphorite in north-eastern Iowa probably represents a condensed interval that correlates with Lithosome I and laterally equivalent parts of Lithosome II in south-eastern Minnesota. Units 1–3 of the trilobite-dominated biofacies can be correlated with Lithosome III and the upper part of Lithosome II (see for example Bayer's (1967) measured section for Locality 18 (Bayer Locality F-231)) and with the lower part of the graptolite shales biofacies (including units 1–3 of Witzke and Glenister's (1987, fig. 3) Graf, Iowa section). Finally, Units 4 and 5 probably correlate with Lithosomes III and IV and with the mixed faunas and upper graptolite shales biofacies (in southern Clayton County, Unit 4 may pass southward into strata assignable to Unit 3).

ANATOMICAL TERMINOLOGY

Use of anatomical terminology in this paper is generally consistent with precedents to be found in Sinclair (1940, 1942, 1952), Moore and Harrington (1956) and Van Iken (1992a). Two new terms, both pertaining to test features of *Conularia*, are introduced here. As indicated by inspection of sectioned and broken material, the interspaces (the regions between the crests of the transverse ribs) of most currently recognized species of *Conularia* are longitudinally corrugated (Pl. 3, figs 1, 3). The crests of the corrugations (as seen viewing the test's exterior surface) will be referred to as interspace ridges, while the troughs between the crests will be referred to as interspace furrows.

SYSTEMATIC PALAEOLOGY

Phylum CNIDARIA Hatschek, 1888

Class, Order, Family Uncertain

Genus SPHENOTHALLUS Hall, 1847

Sphenothallus sp.

Plate 1, figure 8; Plate 2, figure 1

Material. SUI 84486, 84493b, 84495i–k, 84496, 84497a, 84498, 84499a, 84500, 84514e–f, 84517b (> 50 specimens).

EXPLANATION OF PLATE 1

Figs 1, 6. *Conularia splendida* Billings, 1866; upper Ordovician, Maquoketa Formation, Elgin Member, Unit 1; near the mouth of Otter Creek in Elgin, Fayette County, Iowa, USA. 1, SUI 49979a; external view of two faces of a flattened but more or less complete specimen; $\times 1.7$. 6, SUI 49979; radial cluster of eight specimens, all of which are oriented parallel to bedding and occur in a grey, pyritic lime mudstone with graptolites and asaphid trilobite fragments; $\times 0.66$.

Fig. 2. *Conularia trentonensis* Hall, 1847; SUI 61508; upper Ordovician, Maquoketa Formation, Elgin Member, ?Unit 3; north-eastern Iowa (Locality 16), USA; external view of two faces of a flattened specimen; $\times 1.6$.

Fig. 3. *Conularia?* sp.; SUI 84491; upper Ordovician, Maquoketa Formation, Elgin Member, Lithosome II; south-eastern Minnesota (Locality 18), USA; internal mould of a partial face and two corners; $\times 2$.

Figs 4, 8. *Climacoconus quadratus* (Walcott, 1879); upper Ordovician, Maquoketa Formation, Elgin Member, Lithosome I; south-eastern Minnesota, USA. 4, SUI 84494; Locality 18; external view of two faces and a corner; $\times 2.6$. 8, SUI 84493a; Locality 19; partial external moulds of two specimens oriented with their apex next to a tubule of *Sphenothallus* sp. (SUI 84493b); $\times 4.3$.

Fig. 5. *Glyptococonularia gracilis* (Hall, 1847); SUI 55065; upper Ordovician, Maquoketa Formation, Elgin Member, mixed faunas biofacies; north-eastern Iowa (Locality 2), USA; external mould of part of a face and two corners; $\times 4.7$.

Fig. 7. *Climacoconus sinclairi* sp. nov.; GSC 94784; upper Ordovician, Maquoketa Formation, Elgin Member, Unit 3; north-eastern Iowa (Locality 11), USA; external view of the holotype; $\times 3.1$.



Horizon and localities. Elgin Member, Lithosome II (Localities 17b and 19), mixed faunas biofacies (Locality 2; bed 8 of Witzke and Glenister (1987, fig. 3)), graptolite shales biofacies (Locality 1).

Description. Partial tubules up to 90 mm long; tubules apatitic, finely lamellar, preserving one or both longitudinal thickenings and, in some cases, small portions of the thin wall between the thickenings; tubules gently tapered and strongly curved near the apical end; holdfasts not preserved.

Remarks. *Sphenothallus* is widely distributed in middle and upper Ordovician strata of North America, where it is represented by at least two species, *S. angustifolius* Hall (the type species) and *S. splendens* (Hall) (Bolton 1994). The Elgin Member specimens, while similar to these two species in size and gross anatomy, are not sufficiently complete to allow detailed comparisons of the thin test wall between the longitudinal thickenings. As indicated by previous discussions of *Sphenothallus* morphology (e.g. Mason and Yochelson 1985; Van Iten *et al.* 1992; Bolton 1994), this relatively delicate part of the tubule shows interspecific variation in the development of surface ornament. For these reasons, the Elgin Member specimens are here left unassigned at the species level.

It is interesting to note that none of the Elgin Member *Sphenothallus* specimens examined in this study preserves the holdfast. Abundant *Sphenothallus* with holdfasts have been found in mudrocks at several other localities, including the Lower Carboniferous Calciferous Sandstone of Scotland (Slater 1907) and Bear Gulch Limestone of central Montana (Van Iten *et al.* 1992). Some of the specimens from the Calciferous Sandstone are attached to conulariids (*Paraconularia tenuis* (Slater)), while those from the Bear Gulch Limestone commonly are attached to ammonoid shells. In addition to these specimens, abundant non-mineralized holdfasts, similar in gross anatomy and microstructure to mineralized *Sphenothallus* holdfasts, and interpreted by Bodenbender *et al.* (1989) as *Sphenothallus* remains, have been found attached to hardground surfaces in the upper Ordovician Dillsboro Formation of Ohio.

Genus CLIMACOCONUS Sinclair, 1942

Climacoconus sinclairi sp. nov.

Plate 1, figure 7; Plate 2, figure 4; Text-figure 3A

1992a *Climacoconus* sp. Van Iten, p. 341, text-fig. 3g.

Derivation of name. In honour of the late George Winston Sinclair, a leading student of conulariids and author of the genus *Climacoconus*.

Types. Holotype, GSC 94784; paratypes, SUI 61531, 84487; Elgin Member, Units 3 (Localities 5, 11 and 14) and 5 (Locality 10).

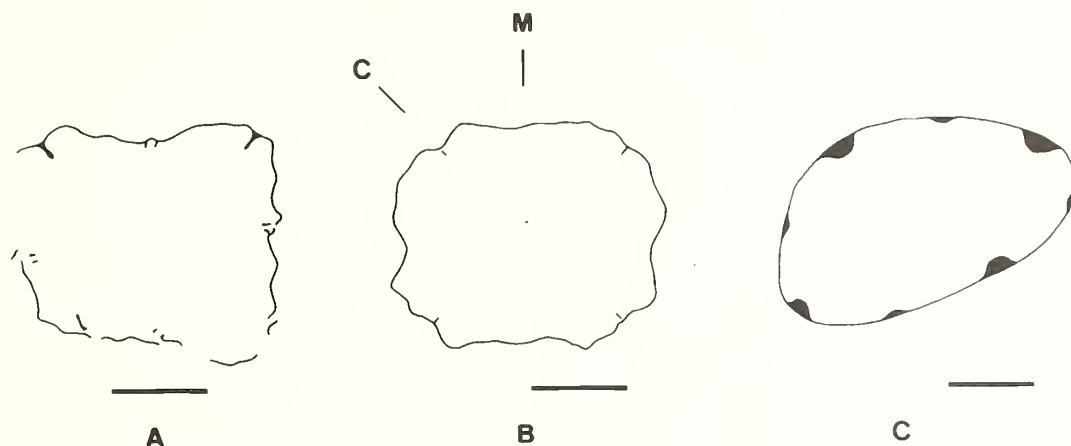
Diagnosis. Midlines straddled internally by a pair of closely spaced, adaperturally diverging files of low, discrete, I-shaped ridges that each extend across an interspace.

Description. Three partial specimens, all broken well above the apex. Corners of a given face diverge at about 14°; corner grooves thickened, carinate; corner carina low, keel-like, darker in colour than the rest of the test; exterior surface of the corner grooves crossed by extremely fine, closely spaced, adaperturally arching transverse wrinkles that number about 25 per mm. Transverse ribs usually alternate at the midlines, straight within about 15 mm of the apex, elsewhere gently curved; transverse ribs increase in size and spacing adaperturally, numbering 6 per 2 mm about 15 mm above the apex and 4 per 2 mm about 25 mm above the apex; transverse ribs offset and deflected toward the aperture on the margins of the corner grooves; within the corner grooves the transverse ribs occur as low, broadly rounded, adaperturally arching ridges that extend approximately two-thirds of the way across the grooves and alternate with ridges projecting from the other side. Midline ridge zigzagged where the transverse ribs alternate, straight where the transverse ribs meet in

opposition; midlines straddled along most of their length by a pair of closely spaced, aperturally diverging files of low, discrete, I-shaped internal ridges, with each ridge extending across an interspace.

Comparisons. *Climacoconus sinclairi* differs from all previously published species of the genus (Sinclair 1942, 1946; Hergarten 1985) in having a pair of seriated internal carinae at the midlines. *C. sinclairi* further differs from *C. bottnicus* (Holm), *C. scoticus* (Lamont) and *C. urbanis* Sinclair in exhibiting alternation of transverse ribs at the midlines, and from *C. batteryensis* (Twenhofel) and *C. bureau* Sinclair in having carinate corners. The new species further differs from *C. quadratus* (Walcott) in having the transverse ribs straighter.

Remarks. The holotype of *C. sinclairi* was described in an unpublished Ph.D. dissertation by Sinclair (1948), who named it *C. clermontanus* (after the village of Clermont, Fayette County, Iowa). The paired files of I-shaped midline ridges are difficult to see in this specimen (the bases of about 15 of the ridges have been exposed through exfoliation), and Sinclair (1948) did not mention them.



TEXT-FIG. 3. Camera lucida drawings of transverse cross sections through Elgin conulariids having internal test structures at their corners (C) and midlines (M). A, *Climacoconus sinclairi* sp. nov.; SUI 61531. B, *Climacoconus quadratus* (Walcott); SUI 84501. C, *Conularia?* sp.; SUI 84490. Scale bars represent 2.5 mm.

The three currently available specimens of *C. sinclairi* were collected from Unit 3. Two additional specimens, now missing, were collected by the senior author from dolostones near the base of Unit 5.

Climacoconus with paired seriated carinae at the midlines also occur in the middle Ordovician Platteville and Decorah formations near Minneapolis, Minnesota (Van Iten 1992a). Reposited specimens are housed in collections of the Geological Survey of Canada (GSC 94785–94786; approximately ten specimens) and the University of Michigan Museum of Paleontology (UMMP 2065; two specimens). Sinclair (1948) assigned the GSC specimens to *C. concinnus* (GSC 94785) or *C. mollis* (GSC 94686), two species erected by Sinclair (1948) but never published. These specimens and UMMP 2065 may represent *C. sinclairi*, but it will be necessary to examine more complete material before making a definitive identification.

Climacoconus quadratus (Walcott, 1879)

Plate 1, figures 4, 8; Plate 2, figure 2; Text-figure 3b

1879 *Conularia quadrata* Walcott, p. 93.

1942 *Climacoconus quadratus* (Walcott); Sinclair, p. 226, pl. 3, figs 1–5.

Material. SUI 62669, 81517–81518, 84492, 84493a, 84494, 84495a–h, 84501–84513, 84514a–d, 84515a–c (84 specimens); WSU unnumbered (six specimens).

Horizon and localities. Elgin Member, Lithosomes I and II (Localities 17b, 18 and 19), Units 1, 4 and 5 (Localities 7 and 9).

Description. Original length of the largest specimen exceeded 80 mm. Faces equal in width or with one set of opposing faces up to about 1.5 times as wide as the other two. Corners of a given face diverge at about 12–15°; corner grooves thickened, carinate; corner carina low, keel-like. Midlines also carinate; midline carina extremely low. Transverse ribs generally alternate at the midlines; transverse ribs in the apical region straight, rounded, meeting at the midlines at about 140°; elsewhere the transverse ribs have sharp crests, are gently curved and intersect the midlines at about 90°; transverse ribs increase in size and spacing adaperturally, with 12 per mm near the apex and 1 or 2 per mm approximately 80 mm above the apex; transverse ribs slightly offset on the margins of the corner grooves, deflected toward the aperture within the grooves and occurring there as low, broadly rounded, adaperturally arching ridges that extend about two-thirds of the way across the grooves and alternate with ridges extending from the other side. Midline ridge zigzagged in the apical region, becoming straighter adaperturally. Exterior of the test crossed by low, closely spaced transverse wrinkles, barely perceptible in the apical region and increasing in size and spacing adaperturally; wrinkles gently arched on the faces, strongly arched in the corner grooves.

Remarks. *Climacoconus quadratus* (Walcott), originally described from the Trenton Group (middle Ordovician) of New York (Walcott 1879), was interpreted by Van Iten (1992a) as having non-carinate midlines. Comparison of broken type specimens of this species with specimens from the Elgin Member indicates that this conclusion probably was incorrect.

Climacoconus pumilus (Ladd, 1929)

Plate 2, figures 5–6; Text-figure 3c

1929 *Conularia pumila* Ladd, p. 384.

1942 *Climacoconus pumilus* (Ladd); Sinclair, p. 231, pl. 2, fig. 10.

Material. UWBM 73175–73176 (45 specimens).

Horizon and locality. Elgin Member, basal Maquoketa phosphorite (Locality 15).

EXPLANATION OF PLATE 2

Fig. 1. *Sphenothallus* sp.; SUI 84486; upper Ordovician, Maquoketa Formation, Elgin Member, graptolite shales biofacies; north-eastern Iowa (Locality 1), USA; tubule preserving portions of both longitudinal thickenings; $\times 12.2$.

Fig. 2. *Climacoconus quadratus* (Walcott, 1879); SUI 84492; upper Ordovician, Maquoketa Formation, Elgin Member, Lithosome II; south-eastern Minnesota (Locality 17b), USA; inner surface of a minute test fragment exhibiting part of a low internal carina at a midline; $\times 40$.

Fig. 3. *Metaconularia heymani* (Foerste, 1920); SUI 62672; upper Ordovician, Maquoketa Formation, Elgin Member, Unit 3; north-eastern Iowa (Locality 7), USA; plastic cast of part of a single face; the centre of the area shown here lies approximately 10 mm above the broken apical end (or roughly 20 mm above the former apex); $\times 30$.

Fig. 4. *Climacoconus sinclairi* sp. nov.; SUI 84487; upper Ordovician, Maquoketa Formation, Elgin Member, Unit 3; north-eastern Iowa (Locality 5), USA; part of a double row of I-shaped internal ridges flanking a midline; $\times 13.2$.

Figs 5–6. *Climacoconus pumilus* (Ladd, 1929); upper Ordovician, Maquoketa Formation, Elgin Member, basal Maquoketa phosphorite; north-eastern Iowa (Locality 15), USA. 5, UWBM 73175a; relatively large specimen; $\times 30$. 6, UWBM 73175b; broken apical end of specimen showing the internal carina (arrows) at the corners; $\times 80$.

All are scanning electron micrographs.



Description. Specimens about 1.0 to 2.5 mm long, broken at both ends but with the apical end commonly less than 0.1 mm wide. Faces equal in width or with one pair of opposing faces slightly wider than the other two. Corners of a given face diverge at about 9–10°; corner grooves narrow, angular, carinate; corner carina low, keel-like. Transverse ribs straight, rounded, alternating at the midlines and numbering 8–9 per mm. Midlines lack internal thickening, zigzag midline ridge.

Remarks. *Climacoconus pumilus* (Ladd) is similar to the apical region of *C. quadratus* (the three available specimens of *C. sinclairi* sp. nov. do not preserve this region), and as noted above the apertural end of available *C. pumilus* specimens is broken. This raises the possibility that *C. pumilus* represents the apical region of *C. quadratus* or some other species (e.g. *C. sinclairi*) having an internal carina at the corners. At this point, however, we have no grounds for rejecting the hypothesis that *C. pumilus* is a distinct species.

Genus CONULARIA Miller in Sowerby, 1821

Conularia trentonensis Hall, 1847

Plate 1, figure 2; Plate 3, figures 1–2

1847 *Conularia trentonensis* Hall, p. 222, pl. 59, fig. 4a–f.

1991c *Conularia trentonensis* Hall; Van Iten, text-fig. 2.

1992a *Conularia trentonensis* Hall; Van Iten, pl. 1, figs 1, 4.

Material. SUI 61506–61509, 64492, 81515, 84497b, 84499b, 84515d, 84516, 84517a, 84518–84521, 84522a (54 specimens); WSU unnumbered (seven specimens).

Horizon and localities. Elgin Member, Lithosomes I and II (Localities 17a and 18), mixed faunas biofacies (Locality 2; bed 8 or 10 of Witzke and Glenister (1987, fig. 3)), graptolite shales biofacies (Locality 2; bed 3 of Witzke and Glenister (1987, fig. 3)).

Description. Faces equal in width. Corners of a given face diverge at about 15–25°; corners and midlines lack internal thickening. Transverse ribs chevron-like on the faces, confluent at the midlines, where they form a more-or-less distinct angle that ranges from c. 145° to 162°; transverse ribs reduced in height and deflected toward the aperture in the corner grooves, where they consist of a single row of longitudinally elongate nodes; transverse ribs number up to 9 per mm within about 10 mm of the apex, elsewhere from 2 to 5 per mm. Rib nodes on the faces tend to be laterally elongate and widely spaced, numbering 4–9 per mm and separated by a gap that generally ranges from c. 1–1.5 node diameters in length. Interspace ridges commonly narrow, bar-like, about half as wide as the interspace furrows; interspace ridges extend from the base of a node on the transverse rib nearest the aperture to an area between two adjacent nodes on the transverse rib nearest the apex; interspace furrows slightly raised along their axis; interspaces crossed by coarse, closely spaced longitudinal striae in the corner grooves. Apical end of some specimens covered by a schott.

Remarks. *Conularia trentonensis* has been reported widely from the middle Ordovician of North America (Sinclair 1948). Our inspection of museum collections in Canada and the USA indicates that this species is widespread in both the middle and the upper Ordovician, and may also occur in the lower Silurian.

Conularia splendida Billings, 1866

Plate 1, figures 1, 6; Plate 3, figures 3–4

1866 *Conularia splendida* Billings, p. 21.

1927 *Conularia splendida* Billings; Twenhofel, p. 256, pl. 27, fig. 9.

1991a *Conularia splendida* Billings; Van Iten, p. 148, fig. 3.

1991c *Conularia splendida* Billings; Van Iten, text-figs 3, 4a.

1992a *Conularia splendida* Billings; Van Iten, pl. 2, fig. 6.

Material. AC I-1448 (one specimen); CCPC 2122.00, 2128.00 (four specimens); FMNH P16976, P16989, P17011, and P17044 (five specimens); SUI 49978, 49979, 61511–61530, 64478–64480, 64483, 64488–64491, 81516, 84522b, 84523–84535 (113 specimens); UMPC 8919 (one specimen); UWBM 73177 (one specimen).

Horizon and localities. Elgin Member, Lithosome I (Locality 18), Units 1, 2 (Localities 4, 7 and 9) and 3 (Localities 4–8, 12 and 13), graptolite shales biofacies (Localities 1–3; specimens from Locality 2 found in bed 3 of Witzke and Glenister (1987, fig. 3)).

Description. Faces equal in width or with one pair of opposing faces up to about 1.3 times as wide as the other two. Corners of a given face diverge at about 20–30°; corners lack internal thickening. Midlines with internal thickening consisting of a single carina, an adaxially bifid single carina or a pair of carinae; midline thickening commonly marked on the exterior of the test by a narrow band of light or dark colouration. Transverse ribs chevron-like within about 10 mm of the apex, elsewhere usually describing a bell-shaped curve whose central portion commonly is somewhat flattened; transverse ribs commonly offset at the midlines, reduced in height and deflected toward the aperture in the corner grooves, where they consist of a single row of longitudinally elongate nodes; transverse ribs number 5–11 per mm within about 10 mm of the apex, elsewhere 1–5 per mm. Rib nodes on the faces tend to be subhemispherical, closely spaced, numbering 5–13 per mm. Interspace ridges generally low, broad, distinctly wider than the interspace furrows on the faces proper; interspace ridges narrower and more closely spaced near and within the corner grooves; interspace ridges extend from the base of a rib node on the transverse rib nearest the aperture to an area between two adjacent rib nodes on the transverse rib nearest the apex; interspace furrows slightly raised along their axis; interspaces crossed by coarse, closely spaced longitudinal striae in the corner grooves; interspaces crossed by a band of fine longitudinal striae at the midlines. Apical end of some specimens covered by a schott.

Remarks. *Conularia splendida* was previously represented by a single specimen (GSC 2157, the holotype) from the English Head Formation (upper Ordovician) of Anticosti Island, Quebec. It is the only member of the genus *Conularia* known to exhibit a bifid carina or pair of carinae at the midlines.

Conularia? sp.

Plate 1, figure 3; Text-figure 3c

Material. SUI 84490 and 84491 (two specimens).

Horizon and Locality. Elgin Member, Lithosome II (Locality 18; specimens collected by Thomas N. Bayer, Winona State University, Winona, Minnesota).

Description. Two partial specimens, both moderately compressed and broken well above the apex, preserved as weathered casts exhibiting original test material in portions of the corners and midlines. Faces originally about equal in width. Corners of relatively undistorted faces diverge at about 18° on one specimen and about 25° on the other specimen; corners sulcate, external morphology of the corner grooves unknown. Transverse ribs gently arched or chevron-like on the faces, confluent or offset at the midlines; transverse ribs number 3–6 in a length of 2 mm. Interspace ridges moderately broad, in places aligned across the transverse ribs, elsewhere offset, with five ridges in a width of 1 mm on the faces proper; interspace ridges narrower and more closely spaced near and within the corner grooves; apertural end of the interspace ridges marked by a coarse, subhemispherical node. Corners and midlines carinate; carina continuous, broad, rounded; carina at the corners larger (broader and higher) than the carina at the midlines, with the corner carina extending up to roughly one-seventh of the distance to the centre of the test cavity.

Remarks. These specimens are provisionally identified as *Conularia* based on the presence of interspace ridges and nodose transverse ribs similar to those of *C. splendida* and *C. trentonensis*. However, these same features also characterize *Holoconularia* Hergarten, which differs from *Conularia* in having the transverse ribs disrupted and offset in the corner grooves (Hergarten 1985). Establishing the generic affinities of the two Elgin casts will therefore require the discovery of

specimens preserving the corner grooves. The Elgin specimens differ from nearly all recognized members of *Conularia* (e.g. Slater 1907; Bouček 1928; Babcock and Feldmann 1986b; Babcock *et al.* 1987b) and *Holoconularia* (Hergarten 1985) in having a strong internal carina at the corners and midlines. A similar carina occurs at the corners and midlines of *C. albertensis* Reed (Devonian of South America and South Africa; Ulrich 1892, pl. 3, fig. 6a; Knod 1908, pl. 24, figs 1–2, pl. 31, fig. 3; Babcock *et al.* 1987b, fig. 10b), but in this taxon the transverse ribs are always continuous at the midlines (Babcock *et al.* 1987b).

Genus GLYPTOCONULARIA Sinclair, 1952

Glyptoconularia gracilis (Hall, 1847)

Plate 1, figure 5

- 1847 *Conularia gracile* Hall, p. 224, pl. 59, fig. 7.
- 1896 *Conularia gracilis* Hall; Ruedemann, pl. 11, figs 5–6.
- 1897 *Conularia gracilis* Hall; Ruedemann, pl. 2, figs 5–6.
- 1952 *Glyptoconularia gracilis* (Hall); Sinclair, p. 144.
- 1994 *Glyptoconularia gracilis* (Hall); Van Iten, p. 363, pl. 1.

Material. SUI 55065–55066 (two specimens); UMPC 8918, 07745 (two specimens).

Horizon and locality. Elgin Member, lower mixed faunas biofacies (Locality 2).

Description. Four specimens, all fragmentary. Corners sulcate, gently curved, diverging at c. 8°; corner grooves bear a low, broad, internal carina. Faces exhibit numerous, short, straight or adapturally arching transverse ridges that are arranged in longitudinal files, with 4–6 files in a width of 1 mm and 7–9 transverse ridges in a length of 1 mm; lateral margins of the files marked by a low longitudinal ridge.

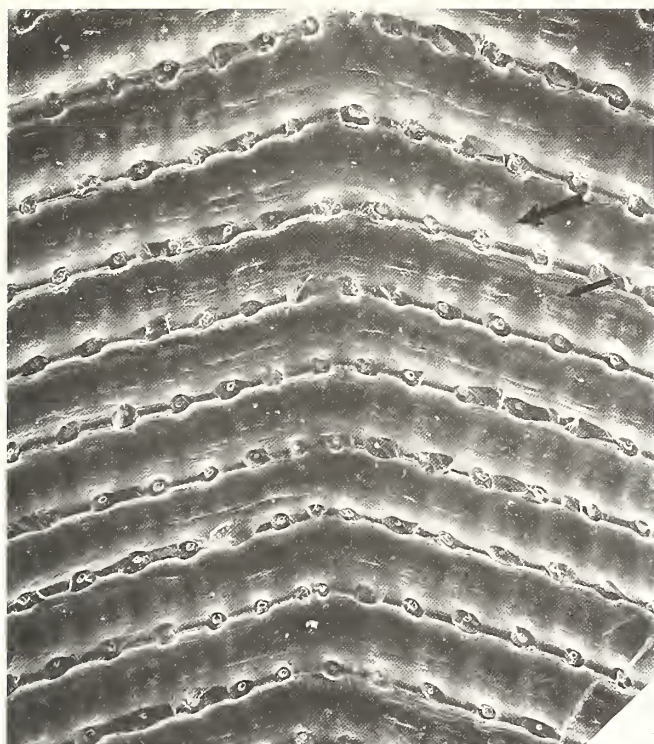
Remarks. *Glyptoconularia* is an extremely rare, monotypic genus currently known from middle and upper Ordovician strata of North America, where it has been found only in dark shales and lime mudstones (Van Iten 1994). Four of the eight repositied specimens of this genus are from brown and grey shales of the Elgin Member at Graf, Dubuque County, Iowa. In addition, we found possible *Glyptoconularia* fragments in acid residues from light grey lime mudstones in Lithosome II. Inspection of type specimens of *Glyptoconularia gracilis* in collections of the American Museum of Natural History, New York (AMNH 789) and the New York State Museum, Albany (NYSM 5063) revealed the presence of a very fine groove along the centre of the ridge bounding the longitudinal files (Van Iten 1994). Although such a groove is not evident in the Elgin specimens, we suspect that this is due to incomplete preservation and/or weathering of the original test material.

EXPLANATION OF PLATE 3

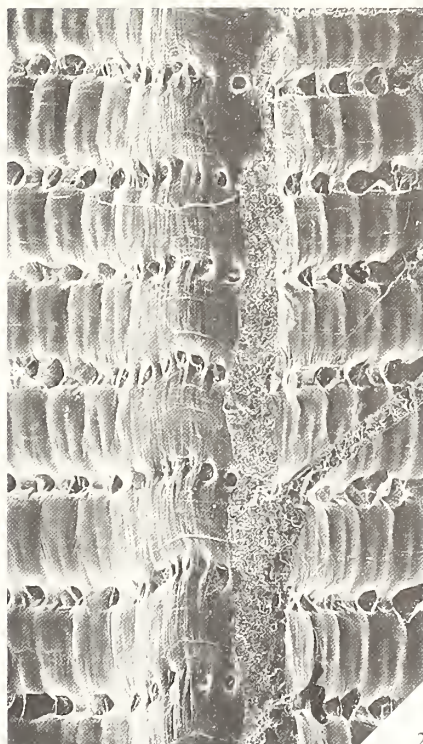
Figs 1–2. *Conularia trentonensis* Hall, 1847; SUI 61507; upper Ordovician, Maquoketa Formation, Elgin Member, ?Unit 3; north-eastern Iowa (Locality 16), USA. 1, part of the external surface of a single face showing the interspace bars (large arrow) and troughs (small arrow). 2, part of the external surface of a single corner groove and adjacent faces. Both $\times 25$.

Figs 3–4. *Conularia splendida* Billings, 1866; upper Ordovician, Maquoketa Formation, Elgin Member, Unit 3; north-eastern Iowa (Locality 7), USA. 3, SUI 61521; a pair of low carinae straddling a midline; $\times 31$. 4, SUI 61530; part of the external surface of a single face showing the interspace bars (large arrow) and troughs (small arrow); $\times 32$.

All are scanning electron micrographs.



1



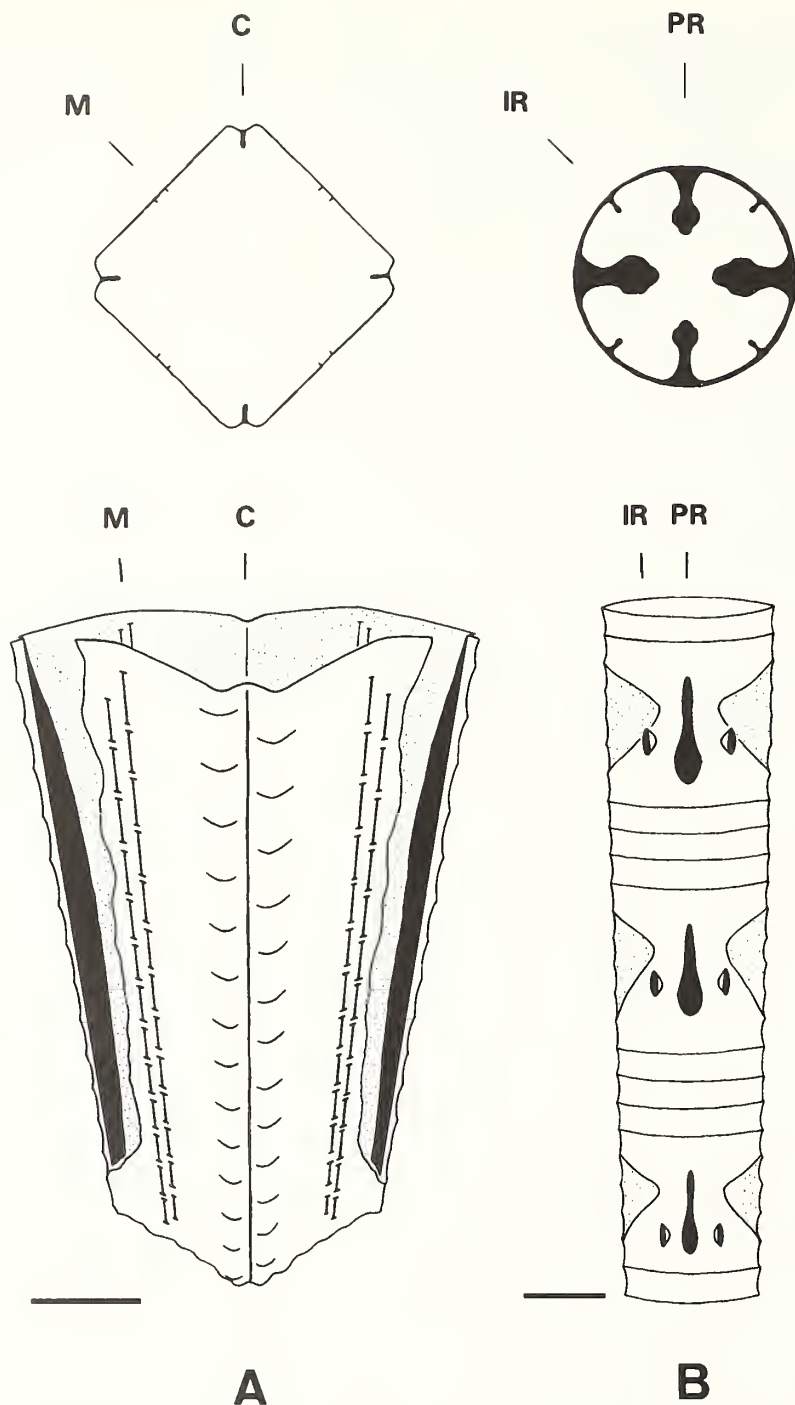
2



3



4



TEXT-FIG. 4. Comparison of the Elgin conulariid *Climacoconus sinclairi* sp. nov. and a theca of the coronatid scyphozoan polyp *Stephanoscyphus racemosus* Werner. A, partial reconstruction (bottom) and transverse section (top) of *Climacoconus sinclairi* showing the single high corner carina and the paired files of low, I-shaped ridges flanking the midlines; scale bar represents 1.5 mm. B, partial theca and transverse section of *Stephanoscyphus racemosus* Werner bearing several whorls of thorn-like internal projections; scale bar represents 1 mm; modified from Werner (1967, fig. 6b).

Genus *METACONULARIA* Foerste, 1928*Metaconularia heymani* (Foerste, 1920)

Plate 2, figure 3

1920 *Conularia heymani* Foerste, p. 208, pl. 21, fig. 12; pl. 22, fig. 12.1928 *Conularia heymani* Foerste; Foerste, p. 110.1940 *Metaconularia heymani* (Foerste); Sinclair, p. 105, pl. 3, fig. 3.

Material. SUI 62672 and 84488 (two specimens); WSU unnumbered (one specimen).

Horizon and locality. Elgin Member, Lithosomes I and II (Localities 17b and 18), Units 1 and 3 (Locality 7).

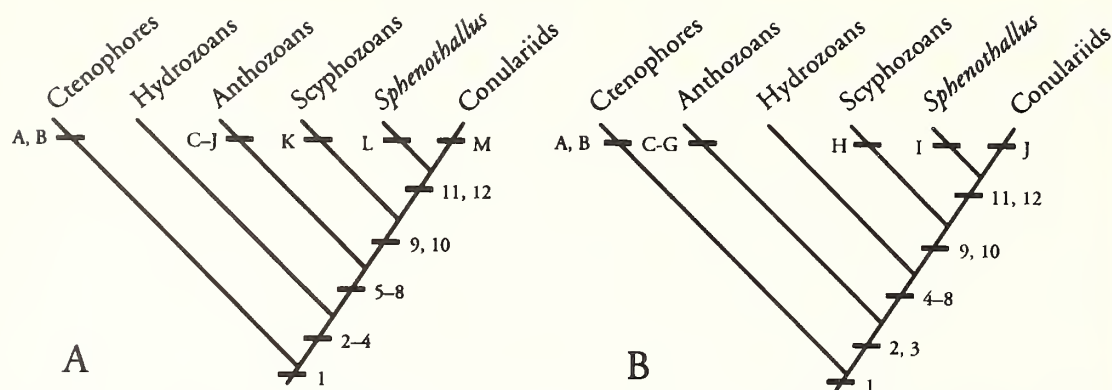
Description. Three specimens, one nearly complete, original length of the largest specimen exceeded 170 mm. Test thin, faces equal in width, corners of a given face diverge at *c.* 30°. Midlines non-sulcate; paired midline carinae low, narrow, diverging at slightly less than 0.5°. Nodes minute, hemispherical to subhemispherical and longitudinally elongate, arranged in transverse rows and longitudinal files, with the transverse rows tending to be more widely spaced than the longitudinal files; transverse rows bell-shaped on the faces, increasing in spacing and decreasing in degree of curvature away from the apex; transverse rows cross the corners and midlines without offset or diminution; transverse rows contain 10–38 nodes per mm, longitudinal files contain 6–23 nodes per mm.

Remarks. This is the first report of *Metaconularia heymani* from strata of late Ordovician age. This species, previously represented by two fragmentary specimens in collections of the United States National Museum, Washington, was first described from the middle Ordovician Plattin Formation near New London, Missouri, USA (Foerste 1920; Sinclair 1940).

CONULARIID CORNERS AND MIDLINES

In a previous article in this journal (Van Iten 1992a), the senior author discussed the anatomy and phylogenetic significance of internal test structures at the corners and midlines of conulariid tests. Among the conulariids reviewed in that article were *Climacoconus sinclairi* (identified as *Climacoconus* sp.; Van Iten 1992a, text-fig. 3G; scale bar in the earlier figure was incorrectly labelled as representing 5 mm; it represented 1 mm) and *Conularia splendida*, both from the Elgin Member. The discovery of an internal carina at the corners and/or midlines of three additional Elgin conulariids (*Climacoconus pumilus*, *C. quadratus* and *Conularia?* sp.) increases the already substantial number of conulariids known to exhibit such structures. Importantly, *Climacoconus quadratus*, *C. sinclairi* and *Conularia?* sp. exhibit an internal carina at both sites (Text-fig. 3). As in most other taxa having carinate corners and midlines, the carina at the corners of the three Elgin species is larger than the carina at the midlines.

Conulariid tests show detailed similarities to non-mineralized thecae of polypoid coronatid scyphozoans (e.g. Werner 1966, 1967; Van Iten 1991a, 1992a, 1992b). For example, the centripetally accreted, inner thecal lamellae of some coronatids are inflected in the perradial and interradian symmetry planes to form eight tetramerally arranged files of thorn-like internal projections (Text-fig. 4B). Projections in the perradial files, interpreted by Werner (1966, 1967) and Van Iten (1991a, 1992a, 1992b) as comparable to sulcate conulariid corners, are consistently larger than projections at the interradian, locally extending nearly all the way to the centre of the thecal cavity. Coronatid polyps possessing internal thecal structures are thus similar to conulariids whose corners and midlines are carinate. This is particularly evident in comparisons of projection-bearing coronatid thecae with the Elgin conulariid *Climacoconus sinclairi* (Text-fig. 4). Together with other uniquely shared similarities involving aspects of thecal structure and growth and damage repair (Werner 1966, 1967; Van Iten 1991a, 1992b; Jerre 1994), these gross anatomical similarities make the class Scyphozoa the best candidate for the nearest extant relative of conulariids (Text-fig. 5).



TEXT-FIG. 5. Cladograms summarizing two alternative hypotheses of phylogenetic relationships among conulariids, *Sphenothallus* and extant cnidarians. The cladograms summarize our interpretations of the affinities of the problematical taxa in the context of the two most widely accepted alternative interpretations of phylogenetic relationships among the extant cnidarian classes (Van Iten 1992c). In both cladograms ctenophorans (Phylum Ctenophora) are interpreted as the nearest living relatives of cnidarians. Many of the synapomorphies (numbered) involve soft-part structures that have not been observed in either conulariids or *Sphenothallus*, but that we infer to have been present in these two taxa based on observable similarities in other anatomical features. Those soft-part synapomorphies that we think can be observed in conulariids and/or *Sphenothallus* are indicated below by round brackets (presence of soft-part structure indicated by hard-part morphology) or square brackets (presence of soft-part structure indicated by relic (pyritized) soft parts; [] = conulariids, []* = *Sphenothallus*). A, cladogram interpreting extant septate cnidarians as members of a monophyletic group that excludes non-septate cnidarians (hydrozoans) (cladogram modified from Van Iten 1992a, text-fig. 8). B, cladogram interpreting hydrozoans and scyphozoans as members of a monophyletic group that excludes anthozoans. Synapomorphies for cladogram A are as follows: 1, diploblastic, tentacle-bearing medusa with a non-septate digestive cavity having four radially disposed primary branches that bear the gonads; 2, cnidae (primitively with operculum and cnidocil); 3, planula larva; [4]*, life cycle with sessile polyp having two or more circumoral tentacles; 5, gastric septa; 6, cnidae-bearing gastric filaments; 7, sex cells ripen in the entoderm; 8, mesenchyme cellular; (9), four septa (e.g. Van Iten 1992a); [10], polydisc strobilation (Van Iten 1991a); 11, theca apatitic; 12, production of schotts that sometimes bear a subcentral dimple or protuberance. Autapomorphies (lettered) for cladogram A are as follows: A, cydippid larva; B, comb rows; C, loss of medusa; D, loss of cnid operculum; E, loss of cnidocil; F, hexaradial and octaradial symmetry; G, actinopharynx; H, siphonoglyph; I, cnidae with tripartite flaps; J, cnidae with special ciliary cones; K, rhopalium; L, apatitic, tubular theca with two longitudinal thickenings; M, apatitic, four-sided steeply pyramidal theca. Synapomorphies (numbered) for cladogram B are as follows: 1, animal diploblastic and with radial symmetry in non-larval forms; 2, cnidae; 3, planula larva; 4, medusa; 5, cnidae with operculum; 6, cnidae with cnidocil; 7, mitochondrial DNA linear (Bridge *et al.* 1992); 8, polyp sheathed in a multilamellar, ectodermal theca having a closed basal attachment disc; (9), four septa; [10], polydisc strobilation (Van Iten 1991a); 11, theca apatitic; 12, production of schotts that sometimes bear a subcentral dimple or protuberance. Autapomorphies (lettered) for cladogram B are as follows: A, cydippid larva; B, comb rows; C, hexaradial and octaradial symmetry; D, actinopharynx; E, siphonoglyph; F, cnidae with tripartite flaps; G, cnidae with special ciliary cones; H, rhopalium; I, apatitic, tubular theca with two longitudinal thickenings; J, apatitic, four-sided steeply pyramidal theca.

Opponents of the hypothesis of a scyphozoan affinity for conulariids (e.g. Kozłowski 1968; Babcock and Feldmann 1986a; Babcock 1991; Yochelson 1991) have generally based their arguments on *differences* between conulariids and scyphozoans, including features purportedly present in conulariids and unique to them, rather than on rigorous demonstration of a set of shared derived *similarities* that support an alternative cladistic hypothesis. As a result of this exclusive focus on differences, advocates of this approach have tended to interpret conulariids as members of an independent extinct phylum. The logic of phylogenetic systematics, however, suggests that one of

three criteria must be met before conulariids can be established either as a new phylum or as non-cnidarians: (1) there are no characters shared by conulariids with any other known phylum (i.e. there is no evidence to support a phylogenetic hypothesis at the phylum level); (2) the most parsimonious cladogram is an unresolved multichotomy, with the relationships of conulariids unresolved with respect to two or more phyla (i.e. the evidence does not allow for a choice among alternative phylum-level hypotheses); or (3) conulariids share a suite of derived similarities with a specific non-cnidarian taxon, and the cladogram depicting that set of relationships is more parsimonious than the cladogram placing conulariids and cnidarians as sister taxa (i.e. the evidence supports a *specific* alternative phylogenetic hypothesis).

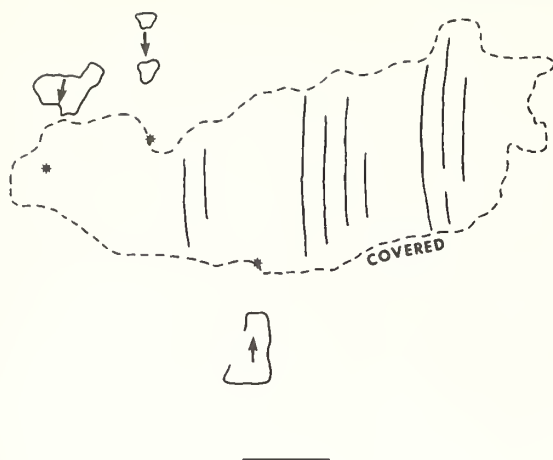
In order to evaluate alternative phylogenetic hypotheses, characters and character states must be rigorously identified, and alternative cladograms must be tested to determine which cladogram is the most highly corroborated by the evidence. Almost without exception, attempts to place conulariids in a separate phylum or remove them from Cnidaria have been based upon negative evidence (the alleged absence of phylogenetically informative characters) or upon an *arbitrary* judgement that the degree of difference between conulariids and other taxa is sufficient to warrant referring conulariids to their own phylum. A major problem has been the excessive focus on conulariid autapomorphies (e.g. Kozłowski 1968; Babcock and Feldmann 1986a), features that are of no use in analysing broader phylogenetic relationships. In the face of numerous similarities identified as being uniquely shared by conulariids and scyphozoan cnidarians (e.g. Kiderlen 1937; Werner 1966, 1967; Van Iten 1991a, 1992a, 1992b; Jerre 1994), in the absence of any demonstration that these similarities fail some critical test of homology (Patterson 1982: including tests of similarity, development, congruity, etc.), and in the absence of any more parsimonious alternative, conulariids must be classified as cnidarians (Text-fig. 5).

PALAEOECOLOGY OF ELGIN MEMBER *SPHENOTHALLUS* AND CONULARIIDS

Evidence of apical attachment in conulariids

A number of investigators (Finks 1955, 1960; Rooke and Carew 1983; Babcock *et al.* 1987b; Harland and Pickerill 1987; Lowenstam and Weiner 1989; Van Iten 1991b; Van Iten and Cox 1992) have presented evidence, some of it (Rooke and Carew 1983; Lowenstam and Weiner 1989) anecdotal, that conulariids were benthic organisms that spent at least part of their lives attached by their apex directly to the sea floor or to biological substrates such as mollusc shells and massive sponges. A similar mode of life has been proposed for *Sphenothallus* (Van Iten *et al.* 1992), based on discoveries of essentially complete *Sphenothallus* specimens attached to shell material together with discoveries of possible *Sphenothallus* holdfasts attached to hardground surfaces. A sessile benthic mode of life for conulariids is indicated most convincingly by two kinds of occurrences: clusters of erect conulariids preserved in Upper Carboniferous black shales (north-central Texas; Rooke and Carew 1983) and Silurian bioherms (north-eastern Illinois; Lowenstam and Wiener 1989); and clusters of conulariids preserved in massive sponges, with the conulariids oriented perpendicular to sponge growth surfaces and expanding (opening) away from the interior of the sponges (western Texas; Finks 1955, 1960; Van Iten 1991b).

Another line of evidence indicating conulariid apical attachment, although not necessarily to benthic substrates, is the occurrence of one or more conulariid specimens next to a piece of non-conulariid shell material in an orientation suggesting original attachment to it (e.g. Babcock *et al.* 1987b, fig. 4c; Van Iten 1991c, text-fig. 1A). This type of occurrence is exhibited by two groups of Elgin Member specimens. One of these groups consists of two specimens of *Climacoconus quadratus* associated with a partial *Sphenothallus* tubule (Pl. 1, fig. 5). The two conulariids, located next to and overlapping each other, are oriented at the same high angle to the tubule, and their apical ends lie on one of its edges. Although the conulariids do not preserve direct evidence of attachment to the tubule (their apices are missing), the probability of obtaining this and other, similar sets of spatial relationships between conulariids and non-conulariid shell material, under the null hypothesis that conulariids were *not* sessile, is essentially zero. The second association consists of four incomplete



TEXT-FIG. 6. *Conularia splendida* Billings; SUI 87728; upper Ordovician (Maquoketa Formation, Elgin Member, Unit 3); north-eastern Iowa (Locality 7), USA; camera lucida drawing of the outlines of three fragmentary specimens preserved next to a straight-shelled nautiloid. Arrows indicate the direction in which a specimen's apical end is pointing. Stars indicate the approximate position of a specimen's apex (now missing). Scale bar represents 20 mm.

specimens of *Conularia splendida* preserved next to a large, flattened, straight-shelled nautiloid (Text-fig. 6). Three conulariids, all located more or less in the same plane as the cephalopod, are oriented approximately perpendicular to the cephalopod's long axis and with their apical ends pointing toward the cephalopod. A fourth specimen, situated slightly below the plane containing the other three, also points toward the cephalopod but is inclined at a much lower angle to the cephalopod's long axis. Again, it is highly improbable that this association, with its multiple, spatial coincidences is fortuitous, particularly in light of previous descriptions of conulariid specimens and shell material showing similar relationships. Rather, it appears likely that these and other Elgin conulariids were attached in life to non-conulariid shell material and, possibly, other substrates.

Monospecific conulariid clusters

Climacoconus quadratus and *Conularia splendida*, two of the most abundant conulariids in the Elgin Member, commonly occur in monospecific clusters. Approximately one-quarter of the 125 specimens of *Conularia splendida* examined in this study occur in discrete, compact clusters of two to eight specimens, all situated within several millimetres of each other. Specimens in five of these clusters (e.g. Pl. 1, fig. 4) converge adapically on a common centre. Similar radial clusters (Van Iten and Cox 1992) have been documented from several other localities in the Palaeozoic of North America and Europe (e.g. Slater 1907, pl. 2, fig. 1; Ruedemann 1925, pl. 22, fig. 3; Sinclair 1940, pl. 2, fig. 5; Babcock and Feldmann 1986a, fig. 4), and have generally been interpreted as former life clusters formed either by clonal budding or by preferential larval settlement (Van Iten and Cox 1992). All of the Elgin Member radial clusters are from Units 1 and 3 of the trilobite-dominated biofacies. Coupled with evidence that conulariids were both sessile and benthic organisms, the occurrence of radial clusters in these two Elgin units suggests that *C. splendida* may have lived on the distal, dysoxic portion of the Elgin carbonate shelf. Had *C. splendida* been transported to this area from other parts of the shelf, then any life clusters probably would have been broken up during transport, and thus fossil remains showing radial arrangements would not occur in Units 1 and 3. Alternatively, Babcock and Feldmann (1984, 1986b) proposed that conulariids were planktonic or pseudoplanktonic organisms, an interpretation that implies that radial clusters preserved in dark mud rocks settled to the sea floor from the overlying water column. Evidence offered in support of this hypothesis consists of the observation that many conulariid species are widespread geographically or occur in strongly dissimilar lithofacies (Babcock and Feldmann 1986b), and also includes the discovery of a radial cluster of *Paraconularia chesterensis* (Worthen) associated with possible planktonic plant remains (Babcock and Feldmann 1986b, fig. 4). Although planktonic taxa generally do exhibit broad geographical ranges and/or occur in dissimilar facies, these observations

alone do not constitute sufficient evidence of a planktonic or pseudoplanktonic lifestyle, for they do not rule out the hypothesis that conulariids were sessile benthic organisms capable of tolerating a wide range of bottom conditions.

Distribution of Sphenothallus and conulariids

Additional evidence bearing on the mode of life of conulariids and *Sphenothallus* is provided by statistical analysis of the distribution of collected Elgin fossils. As shown in Table 1, conulariids occur in all four Elgin biofacies, as does *Sphenothallus*. However, chi-square analysis of the data for

TABLE 1. Stratigraphical distribution and frequency of occurrence of collected Elgin Member *Sphenothallus* and conulariid macrofossils. Unit abbreviations: BMP, basal Maquoketa phosphorite; GSF, graptolite shales biofacies; MFF, mixed faunas biofacies; U1–U5, Units 1–5; LI–LIV, Lithosomes I–IV; LIIA, Lithosome II laterally equivalent to LI (Locality 19); LIIB, Lithosome II stratigraphically superior to LI (Localities 17 and 18). Underlined units are in the brachiopod-echinoderm biofacies, while units in brackets make up the trilobite-dominated biofacies. The letter symbol 'P' means the presence of a taxon in a unit is indicated by test fragments obtained from formic acid residues.

Taxon	Unit												
	BMP	GSF	MFF	[U1]	[U2]	[U3]	U4	U5	[LI]	LIIA	LIIB	LIII	LIV
<i>Sphenothallus</i> sp.	0	4	6	0	P	P	0	0	0	50+	1	0	0
<i>Climacoconus pumilus</i>	45	0	0	0	0	0	0	0	0	0	0	0	0
<i>Climacoconus quadratus</i>	0	0	0	1	0	0	12	7	6	32	32	P	0
<i>Climacoconus sinclairi</i>	0	0	0	0	1	2	0	2	0	0	0	0	0
<i>Conularia splendida</i>	0	4	1	33	1	84	0	0	2	0	0	0	0
<i>Conularia trentonensis</i>	0	30	7	0	0	0	0	0	9	2	6	7	0
<i>Conularia?</i> sp.	0	0	0	0	0	0	0	0	0	0	2	0	0
<i>Glyptoconularia gracilis</i>	0	4	0	0	0	0	0	0	0	0	P	0	0
<i>Metaconularia heymani</i>	0	0	0	1	0	1	0	0	1	0	P	0	0
Totals	45	42	14	35	2	87	12	9	18	84+	41	7	0

TABLE 2. 3×3 matrix for *Climacoconus quadratus*, *Conularia splendida* and *Conularia trentonensis* macrofossils collected from the brachiopod-echinoderm, trilobite-dominated and graptolite shales/mixed faunas biofacies. Application of the chi-square statistic to certain 2×2 contingency tables (e.g. *Climacoconus quadratus* and *Conularia splendida* in the brachiopod-echinoderm and trilobite-dominated biofacies) derived from the 3×3 matrix shows that the observed differences in the proportions of these three conulariids between the rock units are mostly highly significant, ruling out the null hypothesis that the distribution of these conulariids is independent of facies.

Example 2×2 comparison: for the proportions of *Climacoconus quadratus* and *Conularia splendida* macrofossils collected from the brachiopod-echinoderm and trilobite-dominated biofacies.

chi-square = $210(120(83))^2/(90)(120)(83)(127) = 182.99 \gg 6.635$, the chi-square value for the 0.01 level of probability.

	Brachiopod- echinoderm	Trilobite- dominated	Graptolite shales/mixed faunas	Totals
<i>Climacoconus quadratus</i>	83	7	0	90
<i>Conularia splendida</i>	0	120	5	125
<i>Conularia trentonensis</i>	15	9	37	61
Totals	98	136	42	276

conulariids reveals that the distribution of *Climacoconus quadratus*, *Conularia splendida* and *C. trentonensis* is facies-dependent (Table 2). Observed differences in the proportions of these three taxa between the mutually equivalent Elgin biofacies are statistically significant at the 0.01 probability level. For example, 83 of the 102 conulariid macrofossils collected from the brachiopod-echinoderm biofacies (Units 4 and 5 and Lithosomes II and III) represent *Climacoconus quadratus* (the remaining 19 specimens are either *Conularia?* sp. or *Conularia trentonensis*). In contrast, 120 of the 142 conulariid macrofossils collected from the trilobite-dominated biofacies (Units 1–3 and Lithosome I) are *Conularia splendida*. Only seven of these 142 specimens belong to *Climacoconus quadratus*. Similarly, 42 of the 46 conulariids collected in the Dubuque, Iowa area from the graptolite shales and lower mixed faunas biofacies also belong to *Conularia*, although 37 of these represent *C. trentonensis*. Not one of the 46 Dubuque area specimens represents *Climacoconus*. Differences in the proportions of *Climacoconus* and *Conularia* specimens are apparent in acid residue samples as well (Appendix 2). Whereas nearly all of the approximately 275 conulariid test fragments from Lithosome II represent *Climacoconus* or *Conularia trentonensis*, the 108 fragments from the trilobite-dominated biofacies consist predominantly of *Conularia*, probably *C. splendida* (as indicated by the relatively small size and close spacing of the rib nodes). Assuming that *Climacoconus* and *Conularia* had similar preservation potentials (as suggested by their similar test architectures and identical, chemically stable phosphatic composition), these results suggest that the proportions of the different conulariid taxa in the macrofossil samples accurately reflect the original relative abundances of these taxa in the Elgin sea. In addition, the fact that 19 of the 20 limestone blocks sampled here contained conulariid test fragments further suggests that conulariids are ubiquitous in the Elgin limestones.

Although the mode of life of fossil taxa probably can not be inferred from their distribution patterns alone (Klapper and Barrick 1978), the distribution patterns here observed are consistent with the hypothesis that conulariids were sessile benthic organisms, and they tend to falsify certain alternative interpretations of conulariid palaeoecology, in particular models interpreting conulariids as passive floaters or active swimmers living high in the water column. If conulariids were planktonic or nektonic and the distribution of conulariid taxa in life was independent of water depth and distance from the shoreline, the distribution of conulariid fossils would be independent of facies (all other factors being equal). If on the other hand the distribution of planktonic or nektonic conulariids was dependent on water depth and/or distance from the shoreline, the distribution of conulariid taxa could be facies-dependent (see for example Klapper and Barrick 1978, fig. 2a). The observation that *Climacoconus* is extremely rare in the sample from the trilobite-dominated biofacies and absent in the graptolite shales and mixed faunas samples, suggests that the observed distribution of Elgin conulariids cannot be attributed to simple depth segregation. If conulariid taxa were so segregated, with *Climacoconus quadratus* restricted to the oxic (upper) water mass and *Conularia splendida* occurring below this layer, one would expect to find substantial numbers of *Climacoconus* fossils in strata equivalent to the oxic-water brachiopod-echinoderm biofacies. Similarly, it is difficult to interpret Elgin conulariids as swimming or floating organisms subject to lateral segregation. Neither hypothesis, for example, offers a plausible explanation of how remains of originally planktonic or nektonic *Conularia trentonensis* could be present in oxic shelf and basin slope deposits but absent in deposits (Units 1–3) that formed in areas located between these two environments. In summary, then, the stratigraphical distribution of Elgin conulariids suggests that their distribution in life was controlled by bottom conditions, as might be expected had the conulariids lived on the sea floor or very close to it.

From this conclusion it follows that conulariids and, possibly, *Sphenothallus* were eurytopic taxa, capable of living in bottom environments where the concentration of dissolved oxygen may have been too low to support benthic invertebrates (e.g. echinoderms, bryozoans and articulate brachiopods) originally present in bottom waters located closer to the palaeoshoreline. In certain parts of the trilobite-dominated and graptolite shales biofacies, the only macrofossils present are nautiloids, asaphid trilobites and conulariids (*Isotelus iowensis*, *Anataphrus vigilans* and *Conularia splendida*; uppermost part of Unit 1, north-eastern Fayette County, Iowa; see also Calvin 1906,

p. 100) or inarticulate brachiopods, conulariids and *Sphenothallus* (certain grey shale horizons in the graptolite shales biofacies). Together with evidence suggesting that conulariids and *Sphenothallus* were sessile benthic organisms, the presence of these taxa in dark mudrocks lacking echinoderms and articulate brachiopods, taxa that are abundant in laterally equivalent shallow shelf strata, suggests that the problematical cnidarians inhabited dysoxic bottom environments. If the conulariid and *Sphenothallus* specimens now present in dysoxic facies were transported from the shallow shelf, then remains of other shelf taxa should also occur in these beds. Since the dysoxic facies generally do not contain such fossils, but do contain benthic invertebrates (*Lingula*) not present in more proximal deposits, the presence of conulariids and *Sphenothallus* in dark mudrocks of the trilobite-dominated, mixed faunas and graptolite shales biofacies probably cannot be attributed to transport from more proximal bottom environments. Therefore, unless Elgin Member *Sphenothallus* were attached in life to floating objects or to planktonic or nektonic organisms, the most likely explanation of the occurrence of conulariids and *Sphenothallus* in the distal Elgin Member facies is that these organisms originally inhabited dysoxic bottom waters of the shelf margin and basin slope environments.

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APPENDIX 1

Selected collecting localities

1. Elgin Member, basal Maquoketa phosphorite and graptolite shales biofacies; active quarry (Riverside Stone Company) near Highway 20 in south-west Dubuque, Dubuque County, Iowa (NW1/4 NW1/4 sec. 33, T. 89 N., R. 2 E., Dubuque South, Iowa Quadrangle).
2. Elgin Member, graptolite shales and mixed faunas biofacies; road-cut on north-west side of gravel road, about 0.4 km south-west of Graf, Dubuque County, Iowa (near centre S1/2 NW1/4 SW1/4 sec. 29, T. 89 N., R. 1 E., Epworth, Iowa Quadrangle).
3. Elgin Member, graptolite shales biofacies; abandoned quarry in Osborne Park/Nature Center (Clayton County, Iowa), about 200 m east-north-east of State Highway 13 bridge over Volga River (quarry exposes upper part of Dubuque Formation and lower Elgin Member, with contact between these units occurring roughly 6 m above quarry floor; near centre NE1/4 SW 1/4 sec. 9, T. 92 N., R. 5 W., Elkader, Iowa Quadrangle).
4. Elgin Member, basal Maquoketa phosphorite, Units 1–3; abandoned quarry on east side of north–south gravel road, about 2 km north of Big Springs Trout Hatchery, Clayton County, Iowa (quarry exposes contact between Maquoketa and Dubuque formations; near western edge NW1/4 NW1/4 sec. 26, T. 94 N., R. 6 W., Gunder, Iowa Quadrangle).
5. Elgin Member, Units 2–4; roadcut and abandoned quarry on south-east side of County Road B64, about 5.6 km east-south-east of Elgin in extreme north-west Clayton County, Iowa (W1/2 SE1/4 SW 1/4 sec. 16 (road-cut) and E1/2 NE1/4 NW1/4 sec. 21 (road-cut and quarry), T. 94 N., R. 6 W., Gunder, Iowa Quadrangle).
6. Elgin Member, Units 3–5; road-cut and small abandoned quarry on east side of gravel road, about 4 km east-south-east of Elgin in extreme north-west Clayton County, Iowa (SE1/4 SW1/4 SW1/4 sec. 17, T. 94 N., R. 6 W., Gunder, Iowa Quadrangle).
7. Elgin Member, Units 1–4; road-cut on north-east side of County Road B64, about 1.6 km east-south-east of Elgin along the Fayette/Clayton County line, Iowa (E1/4 SE1/4 sec. 13, T. 94 N., R. 7 W., Elgin, Iowa Quadrangle).
8. Elgin Member, Units 3 and 4; small abandoned quarry in hillside overlooking east bank of Turkey River, about 2 km north-north-east of Elgin, Fayette County, Iowa (Gilbertson Wildlife Area; NE1/4 SW1/4 SW1/4 sec. 12, T. 94 N., R. 7 W., Gunder, Iowa Quadrangle).
9. Elgin Member, Unit 1; stream-cut near mouth of Bell Creek, about 1.6 km south of Clermont, Fayette County, Iowa (SW 1/4 SW 1/4 SW1/4 sec. 3, T. 94 N., R. 7 W., Elgin, Iowa Quadrangle).
10. Elgin Member, Units 4 and 5; road-cut on north-east side of gravel road along Bell Creek, next to bridge over Bell Creek and about 1.6 km south-south-west of Clermont, Fayette County, Iowa (N1/2 SE1/4 SE1/4 sec. 4, T. 94 N., R. 7 W., Elgin, Iowa Quadrangle).
11. Elgin Member, Units 3–5; road-cut on south-east side of Highway 18 near base of Montauk Hill, Clermont, Fayette County, Iowa (near centre E1/4 NE1/4 NE1/4 sec. 34, T. 95 N., R. 7 W., Castalia, Iowa Quadrangle).
12. Elgin Member, Unit 3; stream-cut on north-east side of eastward-flowing tributary of Fitzgerald Creek, about 6.4 km north-north-west of Clermont, Fayette County, Iowa (near centre SE 1/4 sec. 8, T. 95 N., R. 7 W., Castalia, Iowa Quadrangle).
13. Elgin Member, Units 3 and 4; road-cut on south-east side of County Road W42, about 13 km north-north-east of West Union, Fayette County, Iowa (SW1/4 NW1/4 SW 1/4 sec. 3, T. 95 N., R. 8 W., Festina, Iowa Quadrangle).
14. Elgin Member, Unit 3; road-cut on north-west side of gravel road, about 0.4 km west of bridge over Dibble Creek and about 9 km north-north-east of Clermont, Fayette County, Iowa (near centre NE1/4 sec. 2, T. 95 N., R. 7 W., Castalia, Iowa Quadrangle).
15. Elgin Member, basal Maquoketa phosphorite; active quarry (exposing Dubuque Formation as well as lower Maquoketa Formation) on east side of Highway 51, about 5 km north of Postville, Allamakee County, Iowa (SW 1/4 SW 1/4 SW 1/4 sec. 16, T. 96 N., R. 6 W., Frankville, Iowa Quadrangle).
16. Elgin Member, Lithosomes I and II; active quarry (Bigalk Quarry) 9.6 km north of north-east corner of Cresco, Howard County, Iowa (near north-west corner sec. 24, T. 100 N., R. 7 W., Cresco NE, Iowa Quadrangle).
- 17a–b. a, Elgin Member, Lithosome I; road-cut on north side of gravel road, approximately 0.5 km west-north-west of Granger, Fillmore County, Minnesota (SW1/4 NW 1/4 sec. 34, T. 101 N., R. 11 W.,

Greenleafon, Minnesota-Iowa Quadrangle). b, Elgin Member, Lithosome II; road-cut on north side of gravel road, approximately 1 km west-north-west of Granger, Fillmore County, Minnesota (NE1/4 NE1/4 sec. 33, T. 101 N., R. 11 W., Greenleafon, Minnesota-Iowa Quadrangle).

18. Elgin Member, Lithosomes I and II; bluff and ravine along east bank of Upper Iowa River, approximately 3 km west of Granger, Fillmore County, Minnesota (SW1/4 SW1/4 SE1/4 sec. 32, T. 101 N., R. 11 W., Greenleafon, Minnesota-Iowa Quadrangle).

19. Elgin Member, Lithosome II; active quarry (Rifle Hill Quarry) and road-cuts approximately 11 km east of junction of US Highway 63 and Fillmore (Minnesota) County Road 14, Fillmore County, Minnesota (NE1/4 NW1/4 sec. 35, T. 102 N., R. 12 W., Greenleafon, Minnesota-Iowa Quadrangle).

APPENDIX 2

Numbers of *Sphenothallus* and conulariid test fragments recovered from one kilogramme Elgin limestone slabs digested in formic acid. Letter symbols are as follows: N_{sp} , number of *Sphenothallus* fragments; N_{Cl} , number of *Climacoconus* fragments; N_{Co} , number of *Conularia* fragments; N_{Gl} , number of *Glyptoconularia* fragments; N_{Me} , number of *Metaconularia* fragments. Number in brackets behind the first, or stratigraphically lowest sample (numbered 0) from a given locality is the height in metres of that sample above the base of the unit or lithosome from which it was collected. All other sample numbers correspond to the approximate height of a given sample above the lowest sample. Additional phosphatic test material recovered from Elgin Member limestone samples consisted of conodonts and is not included in this table.

Locality/sample	Unit	N_{sp}	N_{Cl}	N_{Co}	N_{Gl}	N_{Me}	Total
4/0 [1 m]	Unit 1	0	0	0	0	0	0
4/1	Unit 1	1	0	0	0	0	1
4/3	Unit 2	1	2	15	0	1	18
4/4	Unit 2	0	3	12	0	0	15
4/5	Unit 3	1	0	5	0	0	6
4/6	Unit 3	0	0	1	0	0	1
4/7	Unit 3	0	2	1	0	0	3
4/9	Unit 3	2	1	56	0	2	61
8/?	Unit 2	2	3	5	0	0	10
16/?	Lithosome III	2	2	112	0	0	114
17/0 [1 m]	Lithosome IIB	0	3	3	0	0	6
17/1	Lithosome IIB	10	0	1	0	0	11
17/2	Lithosome IIB	5	30	3	6	0	44
17/3	Lithosome IIB	1	4	0	2	3	10
17/4	Lithosome IIB	3	16	2	9	0	30
17/5	Lithosome IIB	0	3	0	2	0	5
17/6	Lithosome IIB	0	1	0	0	0	1
19/1 [1 m]	Lithosome IIA	0	1	14	0	0	15
19/2	Lithosome IIA	2	1	1	0	0	4
19/3	Lithosome IIA	10	52	2	3	0	67

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The title should be short and informative, and should normally include fossil group, age and general location (if these are appropriate). It should **not** include the names of new taxa or references to other papers. Avoid using brackets. The title should be centred and typed in capitals, but not in bold type.

Authors' names. Authors' names only (without addresses) should be typed in capitals underneath the title. Lower case italics should be used for *by*, and *and* (if there is more than one author).

Authors' names (with their full addresses) should also be typed **at the end** of the paper on the right-hand side of the page after the reference list. Authors may also include their e-mail address, after their postal address.

e.g.

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THE ABSTRACT

A concise abstract of not more than 200 words is required at the beginning of all papers. An abstract reaches a far wider audience than the journal, and therefore it should summarize results (rather than contents) of the paper. It must mention all new systematic names.

The abstract begins with the heading, ABSTRACT (in capitals), flush to the left-hand margin, followed by a full stop, with text continuing on the same line.

THE MAIN TEXT

Introduction. This does **not** have a heading. The first word (or first two words, if the first word is 'A') should be in capitals.

Headings. There are three orders of heading, represented in the typescript as follows: first-order – capital letters, centred; second-order – lower case italics, flush to the left-hand margin, on a line of their own; third-order – as second order, but followed by a full-stop with text continuing on the same line.

Where a list of items is to appear in the running text, each item in the list should be preceded by an arabic numeral, enclosed in brackets. If each item is to start on a new line, the preceding arabic numeral should be flush to the left-hand margin, followed by a full stop, and without brackets.

Citation of references. References should be cited by the author's name and the date of publication, **without** a comma in between **unless** authorship of a taxon is being indicated. Brackets are used as appropriate, e.g. 'The genus *Orthograptus* Lapworth, 1873 was discussed by Mitchell (1987).' The **page reference** to any quotation must be given; page references are also valuable when referring to a small part of a substantial work. A work with three or more authors (e.g. Carton, Pickwick and Squeers 1964), should be shortened (Carton *et al.* 1964), unless ambiguity results. Consecutive references within the same brackets should be arranged chronologically and separated by a semicolon; for those by the same author, dates should be separated by commas, e.g. (Dickens 1963, 1965; Carton *et al.* 1964). References by the same author, published in the same year should be distinguished by the use of suffixes (in *italics*), e.g. Jones (1913*a*, 1913*b*, 1913*c*).

Authors' surnames with prefixes should be given in full, e.g. d'Orbigny, von Huene, etc. In the reference list, papers by these authors should be listed under ORBIGNY, A. C. V. D. d' and HUENE, F. von, respectively. Exceptions to this rule, e.g. De la Beche (in the reference list as DE LA BECHE, not BECHE, De la), depend upon the country of origin of the author and the nature of the prefix to the surname. The handling editors and Technical Editor will advise on the correct form to use.

References in press (i.e. accepted for publication in their final form) are indicated as such (e.g. Owen in press) and must be included in the reference list at the end of the paper. 'In prep.' references are not permitted and will be deleted by the editors from any typescript submitted.

Personal communications should be abbreviated to pers. comm., e.g. '...nautiloids are also known from this locality (D. Evans, pers. comm. 1994).'

Footnotes are not allowed.

Note that wherever authority and date are cited in the text, including systematic higher categories, a full reference must be given in the list of references at the end of the paper.

Reference to plates and text-figures. References in the text to the author's **own** plates and text-figures should be cited, for example, as Plate 1, figure 2 or (Pl. 1, fig. 2) and Text-figure 4c or (Text-fig. 4c) respectively. Note the use of abbreviations and contractions when reference to figures is given in brackets. **Lower case** should be used for plates and text-figures from other papers, e.g. Jones 1978, text-figure 5, (Smith 1955, pl. 1, fig. 7).

SYSTEMATIC PALAEONTOLOGY

Systematic work is always introduced by the first-order heading, 'SYSTEMATIC PALAEONTOLOGY'. The conventions of the journal regarding a marginal or a central position on the page, the order of the different sections, the format for synonymies, references to illustrations, etc. can be found by consulting recent issues of *Palaeontology* and to the example given below.

Care should be taken to ensure that diagnoses, descriptions, and remarks are kept distinct.

The level of the highest taxon used is at the discretion of the author, but must always be accompanied by author and date.

Institutional abbreviations. The systematic palaeontology section should be preceded by a list of institutional abbreviations, in alphabetical order.

Synonymies. Authors are strongly encouraged to annotate synonymies with the symbols listed in Matthews (1973). Additional information at the end of synonym entries is enclosed in square brackets. Note that it is necessary to include only the first page number of a particular reference within the synonymy list; however, all plate and figure numbers should be listed. Place references prefixed by *non* in chronological order within the synonymy list, rather than listing them at the end.

Open nomenclature. Authors should follow the guidelines given by Matthews (1973) and Bengtson (1988).

Example.

Order PHACOPIDA Salter, 1864
Suborder CHEIRURINA Harrington and Leanza, 1957
Family ENCRINURIDAE Angelin, 1854
Subfamily ENCRINURINAE Angelin, 1854
Genus ENCRINURUS Emmrich, 1844

Type species. *Entomostracites punctatus* Wahlenberg, 1818, from the Wenlock of Gotland, Sweden.

Subgenus ENCRINURUS (ENCRINURUS) Emmrich, 1844

Type species. As for genus.

Encrinurus (*Encrinurus*) *macrourus* Schmidt, 1859
Plate 1, figures 1–10; Plate 2, figures 3–6; Text-figure 4A–C

*1859 *Encrinurus punctatus* var. *macrourus* Schmidt, p. 438.

- .1941 *Encrinurus punctatus* (Wahlenberg) 1821 [sic]; Rosenstein, pl. 2, fig. 4-4b; text-fig. 4A.
 vp.1962 *Encrinurus macrourus* Schmidt; Tripp, p. 469, pl. 65, figs 1, 3-4 (non fig. 2 [= *E. (E.) punctatus*]); pl. 66, fig. 1a-c; pl. 67, figs 2-4 (non fig. 1 [= *E. (E.) cf. intersitus* sp. nov.]); pl. 68, figs 1, 3, ?9 (non fig. 2 [= *E. (E.) cf. intersitus* sp. nov.]).
 p.1972 *Encrinurus (E.) cf. punctatus* 2; Schrank, p. 38, pl. 11, fig. 4 (non figs 1-3, 5-7 [figs 1-2, 7 = paratypes of *E. (E.) ruhneensis* Männil, 1978; figs 3, 5-6 are indet.]).
 non1972 *Encrinurus (E.) cf. punctatus macrourus* Schmidt, 1859; Schrank, p. 42, pl. 12, fig. 6 [? = *E. (E.) ruhneensis*], fig. 7 [? = *E. (E.) punctatus*].

Note that this example is based on a trilobite and thus the taxonomic conventions are those of the International Code of Zoological Nomenclature. Systematic palaeontology in palaeobotanical papers should obviously conform to the guidelines of the *International Code of Botanical Nomenclature*.

Third-order headings appropriate in the systematic palaeontology section are:

Derivation of name (for new taxa).

Type specimen or *Holotype* or *Lectotype*, etc.

Material.

Diagnosis.

Description. Note that for descriptions of vertebrates and plants this may be a second-order (or even first-order) heading, with descriptions of portions of the skeleton/plant headed by second-order and third-order headings.

Remarks.

Distribution or *Stratigraphical range* (if applicable).

REFERENCES

These are listed at the end of the text in alphabetical order of authors' names. Each name should be typed in capitals, with the initials after the surname. Note that there should be a space between initials. The names of Chinese and Vietnamese authors should be given in full, as should those of authors of any other nationality should there be any possibility of confusion.

Illustration numbers should be given only where these fall outside the cited pagination. When a title has been translated or transliterated, the original language should be stated in square brackets at the end. The title also should be in square brackets.

Note that in all titles, initial capital letters are used only for proper nouns and for all nouns in German. For books (including volumes containing collections of papers), publisher, place of publication and number of pages should be given in that order after the title.

For publications in which page numbering of individual parts of a volume begins at page 1, include details of both volume (in bold) and part or fascicle (in brackets). Both volume and part numbers should also be included for each *Monograph of the Palaeontographical Society*.

Memoirs, Bulletins, etc. should be listed as *Memoir of the ...*, *Bulletin of the ...*, etc.

Examples of recommended style are given below.

BOUCOT, A. J. 1981. *Principles of benthic marine paleoecology*. Academic Press, New York and London, xv + 463 pp.

BJERRESKOV, M. 1975. Llandoveryan and Wenlockian graptolites from Bornholm. *Fossils and Strata*, **8**, 1-94, pls 1-13.

DE LA BECHE, H. T. 1846. On the formation of the rocks of south Wales and south western England. *Memoirs of the Geological Survey of Great Britain*, **1**, 1-296.

ELLES, G. L. 1925. The characteristic assemblages of the graptolite zones of the British Isles. *Geological Magazine*, **62**, 337-347.

— and WOOD, E. M. R. 1907. A monograph of British graptolites. Part 6. *Monograph of the Palaeontographical Society*, **61** (297), xcvi-cxx, 217-272, pls 28-31.

FANG YI-TING, LIANG SHI-JING, ZHANG DA-LIANG and YU JIN-LONG 1990. *Stratigraphy and graptolite fauna of Lishuwo Formation from Wuning, Jiangxi*. Nanjing University Publishing House, Nanjing, 155 pp., 29 pls. [In Chinese with English summary].

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- WHITTARD, W. F. 1934. A revision of the trilobite genera *Deiphon* and *Onychopyge*. *Annals and Magazine of Natural History*, (10), **14**, 505–553.
- WHITTINGTON, H. B. 1977. The Middle Cambrian trilobite *Naraoia*, Burgess Shale, British Columbia. *Philosophical Transactions of the Royal Society of London, Series B*, **280**, 409–443.

APPENDICES

These may be used for lists of abbreviations used in text-figures, for lists of characters and data matrices used in cladistic analyses, for locality and museum number information, etc. Where the amount of information to be included in an appendix is substantial, authors should consider depositing the information with the British Library (see below). Advice is available from the Publications Secretary.

EXPLANATIONS OF PLATES, TEXT-FIGURES AND TABLES

These should be typed (double-spaced and in journal style) and placed at the end of the typescript. The appropriate position desired for the insertion of each plate, text-figure and table should be indicated in the right-hand margin of the typescript. Explanations should be brief. If a specimen is illustrated, the museum number and magnification **must** be given.

Examples are given below.

EXPLANATION OF PLATE 1

- Figs 1–2, 4–5. *Ozarkodina crispera* (Walliser, 1964). 1, 4, PM X 1276; loc. 31*b*, sample 31*b*7, foreshore of Severn Estuary, Tite's Point, Gloucestershire; Whitcliffe Formation; Pa element; 1, lateral, and 4, oral views; × 60.
 2, 5, PM X 1263; loc. 24*a*, sample 162/2*, Prior's Frome, Hereford and Worcester; Upper Perton Beds; Pa element; 2, lateral and 5, oral views; × 45.
- Fig. 3. *Ozarkodina* cf. *snajdri* (Walliser, 1964); PM X 1189; loc. 7*a*, sample 7*a*/1, Aston Munslow, Shropshire; Whitcliffe Formation; Pa element, lateral view; × 40.

Note that if all specimens are from the same locality, or at the same magnification, etc., there is no need to repeat information for each figure. The bottom line of the plate explanation could be, for example,

'All specimens from the *magnus* Biozone (Aeronian, Llandovery) Derwenlas Formation, Rheidol Gorge, Dyfed; × 10.'

TEXT-FIG. 1. Generalized terrane map of the Canadian Cordillera.

TEXT-FIG. 2. Bone patterns displayed by an abnormal *Iguanodon* caudal vertebral centrum (MIWG 7320). A, transverse section; B, longitudinal section; C, horizontal section. Scale bar represents 10 mm.

TABLE 1. Synapomorphy scheme for internal nodes of the cladogram shown in Text-figure 3.

TABLES

The typesetting of tables is generally carried out by the printers. The desired alignment of text and figures in all tables should be indicated clearly on the submitted version. Tables that cannot be typeset should be drafted carefully, to the same standards as text-figures. Fold-out tables are not acceptable, because of their prohibitive cost. If a table of larger than page size is essential, it should be arranged for two facing pages.

LINE ILLUSTRATIONS

Maintaining a high standard of line illustration quality is an editorial priority.

General points. Individual parts of a single text-figure should be identified by capitals. These should be added to the original illustration by the author. Preferred style is **sans-serif capitals (Helvetica)** with a (published) size of **2.5 mm (10 pt)**.

If the caption for a figure is long, allowance for its inclusion on the same page should be made. In composing small text-figures, space on the page is best used if the figure is wider rather than long (avoid using long and narrow text-figures); the full width of the page should be used where possible.

Authors should consider amalgamating small text-figures, where possible, in order to ensure the most economical use of the page.

All descriptive lettering should be inserted by the author; **sans-serif (Helvetica)** is preferred. Lettering should have a **minimum size of 1 mm (4 pt) on reduction**. Typewriting is not acceptable on text-figures.

A linear scale may be included.

Hand-drawn text-figures. Original drawings, in black on good-quality white card or drawing film should be submitted with the typescript. They should be no larger than double the publication size (print area on the page in *Palaeontology* is **147 × 200 mm**).

Computer-generated text-figures. The quality of text-figures generated by computer-graphics software packages and submitted to *Palaeontology* is extremely variable. Authors should be certain that the finished product is of higher quality than a hand-drawn alternative before submitting a computer-generated line illustration. Map and fossil outlines in particular are often too broad and lack intricate detail.

If producing text-figures by computer, the following points should be noted.

1. Dot fills should be kept to approximately 100 lines or less per inch. More lines per inch results in poor quality reproduction, especially if the text-figure is to be reduced in size.
2. When filling shapes within an illustration, use conventional fills: e.g. solids, tints, lines or crosshatching. This will help with matching of fills for keys contained within the legend. Always use a postscript fill. Do not use the non-postscript pattern fills contained within a graphics program. These are usually bitmap patterns designed for use on low resolution printers and not for output to film recorders or imagesetters. Note that tints within lineart will generally appear paler than laser printer output when printed.
3. 'Shadowing' of figure borders must be avoided.

Note that computer-generated text-figures can be printed directly from a disk, if submitted as 'Freehand' or 'Illustrator' files, preferably saved in the program's own format. The minimum line weight acceptable in such submissions is 0.25 pt.

PLATES AND TEXT- PHOTOGRAPHS

Maintaining a high standard of plate quality is an editorial priority.

Size. Plate size is **147 × 200 mm**. Where authors have photographs which fill less than a full page, they will be referred to as text-figures. Ideally these should be arranged to have a width of 147 mm. Plates and photographic text-figures are reproduced by the same process. Every effort should be made to ensure that no space is wasted. Wherever possible, plates, rather than photographic text-figures, should be submitted.

Plates and photographic text-figures should be submitted **at publication size**. Magnifications of individual figures should be stated in the caption and **not** indicated by scale bars on the photographs.

Lighting. The convention of lighting fossils from the top left should be followed.

Preparation of photographic prints. Photographs should be sharply focused and printed on glossy paper. They should be of medium contrast, using the range of shades of grey but avoiding extremes of black or white. Artefacts, such as dirt or scratches, should be absent from the prints. All prints on a plate should be of even tone and contrast. Where possible, remove labels from macrofossils before photography. Avoid unsightly backgrounds.

Mounting. Mount prints on clean, black or white board of A4 size, using dry mounting tissue or a non-aqueous glue. Place prints as close together as is reasonable (minimum gutter size between prints is 3 mm). Rectangular prints should have adjacent edges at right angles; they should be mounted parallel both to each other and to the sides of the plate. Spacing should be as uniform as possible. It is important to leave sufficient space for figure numbers/letters. If possible, cut off a small corner at 45° to and, at most, 5 mm from the print edge (removal of the bottom right-hand corner is preferred, where possible).

When it is desirable to remove the background from around a fossil, the print should be carefully trimmed to the edge of the fossil and mounted on clean white or black board. In the latter case, the edge of the fossil can be accurately delimited on roughly trimmed prints using black drafting ink. Remember to blacken the edges of trimmed photographs; white edges to trimmed photographs on a black background are not acceptable.

Each plate and photographic text-figure should be protected by an overlay, attached along the upper edge.

Numbering and lettering on overlays. For plates, figure numbers should normally run consecutively from left to right and from top to bottom of each plate. Numbers should be written in appropriate positions on the overlays, but **not** on the plates themselves. All numbers are added in the required positions by the printers. Lettering and arrows, where necessary, should be added to the overlay. For photographic text-figures, individual prints are lettered (A, B, C, etc.), rather than being numbered. Procedure is the same as for plates, all lettering, arrows, etc. being placed on an overlay, to be added in the required position by the printers.

Identification. **Authors should write at the top on the front of each plate and text-figure (on the original, not on the overlay)** the following, leaving a space for the insertion by the Technical Editor of volume and part number.

Author's name Text-fig. or Plate number *Palaeontology*, Vol. , Part

The title of the paper is not required; it will be added by the Technical Editor only should confusion with figures from another paper be a possibility.

Digital submission. Authors should consult the Technical Editor for advice on the digital submission of plates and 'photographic' text-figures.

ADMINISTRATION

Preservation of types and other specimens. In accordance with the recommendations of the International Codes of Botanical and Zoological Nomenclature, **all** illustrated and described fossils **must** be registered and deposited in an appropriate permanent institution, with staff and facilities capable of ensuring their conservation and availability for future reference in perpetuity. The registered numbers **must** be quoted.

Proofs. Authors will normally receive one proof, for the purpose of correcting printer's errors and **not** for altering the wording or substance of the paper. **Authors will be charged for excessive alterations.** The editors will be responsible only for authors' corrections notified by **return of post.** Whenever possible, photographic proofs of publication quality will also be sent to the authors. On the proofs authors should mark **printer's errors in red, other corrections and alterations in blue.**

Offprints. Fifty free offprints of each paper will be supplied (100 in the case of a published Annual Address to the Association). Additional copies may be purchased in multiples of 50 at prices shown on the order form sent with the proofs to the author (or corresponding author in the case of multiple-authored papers). Such offprints can be mailed to up to three authors.

Order of publication. Papers are published, where possible, in the order in which revised typescripts are received by the Technical Editor from the handling editors. When more papers have been received than can be printed within one part of *Palaeontology*, priority is generally given to those with the earliest date of receipt of the revised version by the handling editor and to those by authors who have adhered to the Notes for Authors and have returned proofs by the date requested.

Note that any volume and part numbers which appear on proofs or on reprint order forms are there for Palaeontological Association and the printer's administrative purposes only, and are not necessarily final.

Within each part of the journal, papers are arranged in the order which is most economical in terms of cost; this order is related to number of offprints ordered.

Deposition of data

The Association uses the scheme run by the British Library, whereby tables of data and other reference material can be deposited with the British Library rather than printed. The deposited material is stored on microfiche, and either microfiche or full-size copies may be obtained from the British Library by applicants (preferably using British Library prepaid coupons) on a standard scale of charges which allows for postage, etc.

The British Library will accept deposited material only through the Publications Committee of the Association; all such material will be referred to as part of a published paper. The published paper will bear a reference to deposited copy with full details of its pagination and means of acquisition, e.g. '... have been deposited with the British Library, Boston Spa, West Yorkshire, UK, as Supplementary Publication No. SUP 14003 (26 pp.)'. Prepaid coupons for such purposes are held by many technical and university libraries throughout the world. They may be purchased from the British Library, Lending Division, Boston Spa, Wetherby, West Yorkshire, LS23 7BQ, UK. Association policy is that neither plates nor formal taxonomic data will be considered for deposition. Authors should indicate and separate those parts of their papers that they propose for deposition; the Publications Committee may also recommend that part of a paper should be deposited rather than printed.

Preparation of copy for deposition. Editors will not undertake the preparation of copy. Copy must be prepared by the author according to the following specifications: (1), copy must be camera ready; (2), maximum page size (including margins) is 240 × 330 mm (preferred page size is A4); (3), tabular matter should be headed descriptively on the first page, with column heading recurring on each page; (4), prefatory text, which should contain the abstract from the parent paper, should be included; and (5), all pages must be numbered consecutively.

Authors with large sections for deposition are advised to consult the Secretary of the Publications Committee for further information.

SPECIAL PAPERS IN PALAEOLOGY

Papers prepared for this journal should follow the style of *Palaeontology*. Note that volumes comprising a number of individually authored papers will probably require a preface and an editorial at the beginning. All *Special Papers* require a contents page. Authors/editors are invited to suggest an appropriate cover illustration from amongst those within the *Special Paper*.

Submission. Prospective authors, and editors of compilations, should consult the Publications Secretary well in advance of submission, supplying as much information as possible (i.e. title, estimated number of type-written pages, plates and text-figures, and probable date of submission).

Cost of publication. The Association's funds for this series are limited. Authors are asked to obtain grants to cover costs wherever possible. Scripts should not normally exceed the equivalent of 150 published pages. The Association endeavours to produce two *Special Papers* per year.

Offprints. Authors of *Special Papers* and editors of compilation volumes will receive ten free copies. Offprints of papers in compilation volumes will be supplied according to the same rules as for papers in *Palaeontology*. Authors may buy extra copies of the complete *Special Paper* at half the published price, as long as the order is placed at the same time as the proofs are returned.

FIELD GUIDES TO FOSSILS

Papers for this series should be prepared in the general style of *Palaeontology*. There are some stylistic differences, however, outlined below.

List of contributors. A list of all contributors, in alphabetical order, with addresses, should precede the contents page.

Abstract. An abstract is not required.

Systematic palaeontology. In order to prevent reference lists from becoming excessively long, authorship of taxa should be indicated, but the date of publication is not required. Readers should be directed to the appropriate monographs, etc. in the introductory section to each chapter dealing with a different fossil group.

Subheadings (e.g. Description, Range, Remarks) should be in **bold type** and not italicized.

It is highly desirable that the **museum registration numbers** of figured specimens are included in figure captions.

References. In multiple-authored volumes there should be one all-inclusive reference list at the end of the guide, rather than separate reference lists for each chapter.

Systematic index. All *Field Guides* require a Systematic Index. Authors/editors are encouraged to produce the entries for this prior to submission. All taxa should be included. Species should be listed twice, as 'genus species' and 'species, genus', e.g. the graptolite species *Spirograptus turriculatus* would have two entries, '*Spirograptus turriculatus*' and '*turriculatus, Spirograptus*'. Within the index, page numbers are referred to in normal type, plates and text-figures in bold type.

Cover. Authors/editors are invited to submit a front cover illustration: a high quality colour slide or negative (together with print) with considerable visual impact is recommended. A brief summary of c. 150 words of the *Field Guide*'s contents, suitable for the back cover and comprehensible to non-specialists, should also be submitted.

Submission. Prospective authors and editors should consult the Publications Secretary well in advance of submission, supplying as much information as possible (i.e. title, estimated number of type-written pages, plates and text-figures, and probable date of submission).

Cost of publication. The Association will cover all publication costs.

Royalties. Any royalties from sales of *Field Guides* go to the Association.

Offprints. Editors of *Field Guides* each receive six copies of the published guide. Chapter authors each receive two copies. Further copies may be obtained at a special reduced charge if ordered in advance of publication.

GRANTS IN AID OF PUBLICATION

Palaeontology has no compulsory page or plate charges. However, authors are requested to seek grants in aid of publication from their institutions or from research funds, or to apply for publication costs in research grants. Such financial support is particularly welcome, especially for the publication of long papers. Acceptance of a paper for publication is in no way dependent on the receipt of such grants; authors will appreciate, however, that the funds available to the Association for publication are limited. Every grant or donation will therefore directly help the Association's publication programme.

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INDEX

A

- Abnormalities: bryozoan, 237; graptolite, 219; trilobite, 236
 Acanthodians: Devonian, Canada, 241
 Acritarchs: Ordovician, 389
Acrodonta irerhi, 909
Adygeya adygensis, 690
 Alberdi, M. T. See Prado, J. L. and Alberdi, M. T.
 Alligators: Cretaceous, Canada, 351
Amicytheridea, 934
 Ammonoids: Devonian, Spain, 149; Jurassic, Spain, 851; Oxfordian, England, 433; Toarcian, North America, 97
 Amphibians: Cretaceous, Sudan, 77; Oligocene salamanders, 477; Triassic temnospondyls, Madagascar, 305
Ancyrochitina sp. nov. A, 647
Angochitina tsegelnjuki, 644; *A. tsegelnjuki*?, 644
'Anomotodon' sp., 836
 Antarctica: Jurassic–Cretaceous bivalves, 615
 Arachnids: Devonian trigonotarbid, 611; Silurian trigonotarbid, 605; solifuges, 583
Archaeolamna haigi, 823; *A. aff. kopingensis*, 823
 Archosaurs: Triassic, 883
Arenigomys carinata, 1018
 Asteroids: Jurassic, England, 179
 Australia: Cretaceous sharks, 813
Autunia, 202
 Axe, L. See Edwards, D., Davies, K. L., Richardson, J. B., Wellman, C. H. and Axe, L.

B

- Bacinella irregularis*, 23
 Ballent, S. See Whatley, R. C. and Ballent, S.
Beltella depressa, 381
 Benton, M. J. and Walker, A. D. *Rhombopholis*, a prolacertiform reptile from the Middle Triassic of England, 765; see also Grange, D. R. and Benton, M. J.
 Biostratigraphy: Jurassic ammonoids, 97, 460, 851; Oligocene–Miocene corals, 536; Ordovician acritarchs, 399; Ordovician graptoloids, 869; Permian, Morocco, 916; Permian plants, China, 192; Silurian–Devonian Chitinozoa, Ukraine, 629
 Bivalves: Carboniferous, Great Britain, 407; Cretaceous, England, 1027; Jurassic–Cretaceous, Antarctica, 615; Ordovician, Wales, 979

- Blake, D. B. Redescription and interpretation of the asteroid species *Tropidaster pectinatus* from the Jurassic of England, 179
 Bolivia: Cretaceous salamander, 89
 Bosellini, F. R. See Budd, A. F., Bosellini, F. R. and Stemmann, T. A.
Brachycormus noachicus, 477
 Brachiopods: Ordovician clitambonitidines, 21; Ordovician–Silurian eospiriferines, 941
 Brand, P. J. Taxonomy and distribution of the Upper Carboniferous non-marine bivalve *Carbonicola aldamii*, 407
 Brazil: Cretaceous solifuges, 583
 Brinkman, D. B. See Wu, X.-c. Brinkman, D. B. and Russell, A. P.
 Brocke, R. See Servais, T., Brocke, R. and Fatke, O.
 Bromley, R. G. See Wetzel, A. and Bromley, R. G.
 Budd, A. F., Bosellini, F. R. and Stemmann, T. A. Systematics of the Oligocene to Miocene reef coral *Tarbellastraea* in the northern Mediterranean region, 515
 Bull, E. E. Implications of normal and abnormal growth structures in a Scottish Silurian dendroid graptolite, 219

C

- Callipteris changii*, 200; *C.? laceratifolia*, 200
 Cambrian: trilobites, 377
 Canada: Cretaceous alligator, 351; Devonian acanthodian fish, 241
 Captorhinid reptiles: Permian, Morocco, 907
Carbonicola aldamii, 407
 Carboniferous: non-marine bivalves, 407; pteridosperms, 561; solifuge, 583
Carcharias sp. A, 841; *C. sp. B*, 842
Carminodonta crossi, 998
Cassidiceps vermiculatus, 250
Celaeceras sp., 152
Celtoconcha foveata, 1002
 China: Ordovician graptoloids, 869; Permian plants, 191
Chiropteris reniformis, 198
 Chitinozoa: Silurian–Devonian, Ukraine, 629
 Christian, A. and Preuschoft, H. Deducing the body posture of extinct large vertebrates from the shape of the vertebral column, 801
 Cladistic analysis: archosaurs, 896; asteroids, 180; bivalves, 615; cnidarians, 1054; eusuchians, 367;

- horses, 663; vertebrates, 259; younginiform diapsid reptiles, 301
- Cleal, C. J., Laveine, J.-P. and Shute, C. H. Architecture of the Upper Carboniferous pteridosperm frond *Macroneuropteris macrophylla*, 561
- Cleionychia* sp., 1016
- Clinacoconus pumilis*, 1046; *C. quadratus*, 1045; *C. sinclairi*, 1044
- Cnidarians: Ordovician, USA, 1037
- Coleoids: Cretaceous spirulids, 681
- Comia*, 201
- Conularia splendida*, 1048; *C. trentonensis*, 1048; *C.?* sp., 1049
- Conulariids: Ordovician, USA, 1037
- Cope, J. C. W. Early Ordovician (Arenig) bivalves from the Llangynog Inlier, South Wales, 979
- Corals: Jurassic, 413; Miocene, 515; Oligocene, 515
- Cox, R. S. See Van Iten, H., Fitzke, J. A. and Cox, R. S.
- Crame, J. A. A new oxytomid bivalve from the Upper Jurassic–Lower Cretaceous of Antarctica, 615
- Cratosolpuga wunderlichi*, 601
- Cretaceous: alligator, 351; amphibians 77; bivalves, 615, 1027; Foraminifera, 44; ostracods, 919; solifuge, Brazil, 583; sharks, Australia, 813; spirulid coleoids, 681
- Cretolamna appendiculata*, 828; *C. gunsoni*, 829
- Cretoxyrhina mantelli*, 819
- Crocodyles: Kimmeridgian, 497
- Cyrtodonta* cf. *staffordae*, 1011; *C. cf. watti*, 1011
- Cyrtodontula* cf. *hadzeli*, 1012
- Czech Republic: Devonian gastropod, 709; Ordovician graptoloids, 869

D

- Dakosaurus lissocephalus*, 510; *D. maximus*, 508
- Davies, K. L. See Edwards, D., Davies, K. L., Richardson, J. B., Wellman, C. H. and Axe, L.
- Decipia decipiens*, 456; *D. lintonensis*, 458; *D. ravenswykensis*, 448
- Deltacephalus whitei*, 305
- Dendroidea: Silurian, 219
- Devonian: acanthodian fish, Canada, 241; ammonoids, Spain, 149; Chitinozoa, Ukraine, 629; gastropod, Bohemia, 709; trigontarbid arachnids, 611
- Diapsid reptiles: Permian, South Africa, 289; Triassic archosaurs, 883; Triassic, Europe, 323
- Dicrodiacrodium ancoriforme*, 392
- Dictyonema pentlandica*, 222
- Dixon, J. A. D. See Wood, R., Dixon, J. A. D. and Kirkland, B. L.
- Doguzhaeva, L. A. Two early Cretaceous spirulid coleoids of the north-western Caucasus: their shell ultrastructure and evolutionary implications, 681

- Dromacythere*, 935
- Dumortieria* cf. *dumortieri*, 126; *D. cf. exacta*, 127; *D. insignisimilis*, 126; *D.?* *phantasma*, 128; *D. cf. pusilla*, 130; *D. raricostata*, 127
- Dunlop, J. A. A trigonotarbid arachnid from the Upper Silurian of Shropshire, 605
- Dutuit, J.-M. See Jalil, N.-E. and Dutuit, J.-M.

E

- Echinoderms: Jurassic asteroids, 179
- Edwards, D., Davies, K. L., Richardson, J. B., Wellman, C. H. and Axe, L. Ultrastructure of *Synorisporites downtonensis* and *Retusotriletes* cf. *coronatus* in spore masses from the Přidolí of the Welsh Borderland, 785
- England: Carboniferous bivalves, 407; Cretaceous bivalves, 1027; Jurassic ammonoids, 433; Jurassic asteroids, 179; Jurassic crocodiles, 497; Jurassic plants, 719; Silurian spores masses, 783; Silurian trigonotarbid, 605; Triassic diapsid reptiles, 323; Triassic palaeonisciform fish, 772; Triassic pro-lacertiform reptile, 763
- Eospirifer praecursor*, 941
- Eotarbust jerami*, 613
- Eurymya* sp., 1010
- Eusuchians, 351
- Evans, S. E., Milner, A. R. and Werner, C. Sirenid salamanders and a gymnophionan amphibian from the Cretaceous of the Sudan, 77; see also Smith R. M. H. and Evans, S. E.
- Extinction patterns: mammals, South America, 651

F

- Falcatodonta costata*, 1013
- Fariña, R. A. See Lessa, E. P. and Fariña, R. A.
- Fastigatocythere*, 931
- Fatke, O. See Servais, T., Brocke, R. and Fatke, O.
- Fish: Cretaceous sharks, Australia, 813; Devonian acanthodians, Canada, 241; 'ostracoderms', 259; Triassic palaeonisciform, England, 772
- Fitzke, J. A. See Van Iten, H., Fitzke, J. A. and Cox, R. S.
- Foraminifera: Cretaceous, 44; image analysis, 471; Jurassic, 21; test geometry, 471; Triassic, 44
- Fortowensi grandis*, 999
- Fugusuchus hejapanensis*, 889
- Functional morphology: trilobite enrolment, 377; vermetid and siliquariid gastropods, 157

G

- Gagnier, P.-Y. and Wilson, M. Early Devonian acanthodians from northern Canada, 241

García-Alcade, J. L. See Montesinos, J. R. and García-Alcade, J. L.
 Gastropods: Devonian, 709; vermetids and siliquariids, 157
 Germany: Jurassic Foraminifera, 23; Triassic diapsid reptiles, 323
Glyptarca serrata, 994
Glyptoconularia gracilis, 1050
Glyptocythere, 926
Glyptogatocythere, 934
 'Glyptograptus' *bohemicus*, 869
Goniophora (*Cosmogoniophora*) *extensa*, 1005
 Gower, D. J. and Sennikov, A. G. Morphology and phylogenetic informativeness of early archosaur braincases, 883; see also Storrs, G. W., Gower, D. J. and Large, N. F.
 Grahn, Y. See Paris, F. and Grahn, Y.
 Grange, D. R. and Benton, M. J. Kimmeridgian metriorhynchid crocodiles from England, 497
 Graptolites: Ordovician graptoloids, 869; Silurian dendroids, 219
 Gymnophiona, 91

H

Hammatoceras insigne, 139; *H. speciosum*, 139; *H. sp. nov.*, 140
Helminthopsis, 1; *H. abeli*, 4; *H. hieroglyphica*, 15; *H. intermedia*, 7; *H. labyrinthica*, 7; *H. magna*, 4
Helminthozyga, 175
 Hewison, R. H. The skull of *Deltacephalus whitei*, a lydekkerinid temnospondyl amphibian from the Lower Triassic of Madagascar, 305
Holcophylloceras calypso, 115
 Horný, R. J. See Peel, J. S. and Horný, R. J.
 Horses, 663

I

Iguanodon, 801
 Image analysis: foraminiferal test geometry, 471
 Insalaco, E. The use of Late Jurassic coral growth bands as palaeoenvironmental indicators, 413
Isastraea explanata, 413

J

Jakobs, G. K. and Smith, P. L. Latest Toarcian ammonoids from the North American Cordillera, 97
 Jalil, N.-E. and Dutuit, J.-M. Permian captorhinid reptiles from the Argana formation, Morocco, 907
 Janvier, P. The dawn of the vertebrates: characters versus common ascent in the rise of current vertebrate phylogenies, 259
Johnlongia allocotodon, 837

Jurassic: ammonoids, 97, 433, 851; asteroids, 179; bivalves, Antarctica, 615; coral growth bands, 413; crocodiles, 497; Foraminifera, 21; ostracods, 919; plants, 719; symbiosis, 21

K

Kababisha humerensis, 81; *K. sudanensis*, 87; *K. sp. indet.*, 87
Kathemacanthus rosulentus, 243
 Kirkland, B. L. See Wood, R., Dixon, J. A. D. and Kirkland, B. L.
 Knight, R. I. and Morris, N. J. Inoceramid larval planktotrophy: evidence from the Gault Formation (Middle and basal Upper Albian), Folkestone, Kent, 1027
 Konijnenburg-van Cittert, J. H. A. van. Two *Osmundopsis* species and their sterile foliage from the Middle Jurassic of Yorkshire, 719

L

Large, N. F. See Storrs, G. W., Gower, D. J. and Large, N. F.
 Laveine, J.-P. See Cleal, C. J., Laveine, J.-P. and Shute, C. H.
 Leinfelder, R. R. See Schmid, D. U. and Leinfelder, R. R.
Leptostyrax sp., 826
 Lessa, E. P. and Fariña, R. A. Reassessment of extinction patterns among the Late Pleistocene mammals of South America, 651
Lithocodium aggregatum, 21
 Loydell, D. K. See Štorch, P. and Loydell, D. K.

M

Macroneuropteris macrophylla, 561
 Madagascar: Triassic temnospondyl amphibians, 305
Magilus, 174
Majungaella, 929
Malzia, 931
 Mammals: horses, 663; Pleistocene, South America, 651
Metaconularia heymani, 1053
Metriorhynchus hastifer, 510; *M. superciliosus*, 498
Microbiplices? *sp.*, 460
 Milner, A. R. See Evans, S. E., Milner, A. R. and Werner, C.
 Miocene: corals, 515
Modiolopsis sp. A; *M. sp. B*
 Montesinos, J. R. and García-Alcade, J. L. An occurrence of the auguritid ammonoid *Celaeceras* in the Lower Devonian of northern Spain, 149
 Moradisaurinae gen. et. sp. indet., 910
Moridunia simplicidens, 1004

Morocco: Permian captorhinid reptiles, 907
 Morris, N. J. See Knight, R. I. and Morris, N. J.
 Multivariate analysis: Oligocene–Miocene corals, 522

N

Naefia kabanovi, 694
 Neoteny: salamanders, 477
Normalograptus persculptus, 869
Noterpeton bolivianum, 89
 Notes for authors. The Editors, 1065
Novocythere, 933
Nystroemia pectiniformis, 196

O

Oligocene: corals, 515; salamanders, 477
 Olóriz, F. and Rodríguez-Tovar, F. J. The ammonite *Sutneria* from the Upper Jurassic of southern Spain, 851
 Ordovician: acritarchs, 389; bivalves, 979; brachiopods, 53, 941; cnidarians, 1037; conulariids, 1037; graptoloids, 869; *Sphenothallus*, 1037; trilobites, 377
Osmundopsis hilli, 720; *O. sturii*, 722
 Ostracods: Jurassic–Cretaceous, 919
 'Ostracoderms', 259
Ovatoconcha fragilis, 989

P

Pachystropheus rhaeticus, 323
 Palaeobiogeography: Devonian ammonoids, 149; Jurassic ammonoids, 97
 Palaeoclimate: Jurassic, 413
 Palaeoecology: Cretaceous bivalves, 1027; Jurassic corals, 413; Jurassic Foraminifera, 21; Ordovician cnidarians, 1055; Permian Capitan reef, 733; Permian diapsid reptiles, 289; Silurian dendroids, 219; trilobites, 377; vermetid and siliquariid gastropods, 157; vertebrate body posture, 801
 Palaeoenvironmental analysis: Jurassic, 413
 Palaeophytogeography: Carboniferous pteridosperm, 574; Ordovician acritarch, 401; Permian, 189
Palaeopteria sp., 1017
Parallelodus dyfedensis, 1008
Paranomotodon sp., 835
 Paris, F. and Grahn, Y. Chitinozoa of the Silurian–Devonian boundary sections in Podolia, Ukraine, 629
Paulinea parva, 985
 Peel, J. S. and Horný, R. J. Sinistral hyperstrophic coiling in a Devonian gastropod from Bohemia with an *in situ* operculum, 709
Peltaspermum sp., 202
Peltura scarabaeoides scarabaeoides, 386

Pensarnia laeviformis, 984
Perisphinctes (Arisphinctes) kirkdalensis, 441; *P. (A.) osmingtonensis*, 451; *P. (A.)* sp. A, 442; *P. (A.)* sp. B, 442; *P. (A.?)* sp.
Perisphinctes (Dichotomosphinctes) aff. elizabethae, 444; *P. (D.)* sp. A, 445; *P. (D.)* sp. B, 445; *P. (D.)* sp. C, 446; *P. (D.)* sp., 451; *P. (D.)* sp. E
Perisphinctes (Perisphinctes) cautisnigrae, 450; *P. (P.) aff. parandieri*, 440; *P. (P.) uptonensis*, 440
Perisphinctes (Pseudarisphinctes) damoni, 455; *P. (Ps.) pachachii*, 452
Perisphinctes (Pseudopomerania) dewari, 446, 455
 Permian: Capitan reef, USA, 733; captorhinid reptiles, Morocco, 907; diapsid reptiles, South Africa, 289; Great Eurasian Floral Interchange, 189; plant fossils, China, 191
 Phylogeny: archosaur, 883; bivalve, 625; brachiopod, 941; cnidarian, 1054; eusuchian, 367; salamander, 477; spirulid coleoid, 681; trigonotarbid arachnid, 610; vertebrate, 259
 Planktotrophy: Cretaceous bivalves, 1027
 Plants: Carboniferous pteridosperms, 561; Jurassic, England, 719; Permian, China, 189
Plateosaurus, 801
 Pleistocene: mammals, South America, 651
Pleydellia aalensis; *P. crassiorata*, 120; *P. maudensis*, 116
 Portugal: Jurassic Foraminifera, 23
 Prado, J. L. and Alberdi, M. T. A cladistic analysis of the horses of the tribe Equini, 663
Praeacuellina umbonoradiata, 620
 Preuschoft, H. See Christian, A. and Preuschoft, H.
Progonocythere, 919
 Prolacertiform reptiles: Triassic, England, 763
Protoblechnum wongii, 201
Protosolpuga carbonaria, 600
Pseudoisurus tomosus, 831; *P.?* sp., 834
Pseudohioceras compactile, 138
Psymphyllum multipartitum, 194
 Pteridosperms: Carboniferous, 561

R

Rapa, 174
 Reptiles: Cretaceous alligator, Canada, 351; Jurassic crocodiles, 497; Permian captorhinids, Morocco, 907; Permian diapsids, South Africa, 289; Triassic diapsids, Europe, 323; Triassic prolacertiform, England, 763
Retusotriteles cf. coronadus, 794
Rhombopholis scutulata, 765
Riberia complanata, 1019
 Richardson, J. B. See Edwards, D., Davies, K. L., Richardson, J. B., Wellman, C. H. and Axe, L.
 Roček, Z. The salamander *Brachycormus noachicus* from the Oligocene of Europe, and the role of neoteny in the evolution of salamanders, 477

- Rodríguez-Tovar, F. J. See Olóriz, F. and Rodríguez-Tovar, F. J.
 Rong, J.-y. and Zhan, R.-b. Brachidia of Late Ordovician and Silurian eospiriferines (Brachiopoda) and the origin of the spiriferides, 941
Rothpletzia rudista, 175
 Rubel, M. See Wright, A. D. and Rubel, M.
 Russell, A. P. See Wu, X.-c. Brinkman, D. B. and Russell, A. P.
 Russia: Cretaceous spirulid coleoids, 681

S

- Savazzi, E. Adaptations of vermetid and siliquarid gastropods, 157
 Schmid, D. U. and Leinfelder, R. R. The Jurassic *Lithocodium aggregatum*–*Troglotella incrustans* foraminiferal consortium, 21
 Scotland: Carboniferous bivalves, 407; Silurian dendroid graptolites, 219
 Selden, P. A. and Shear, W. A. The first Mesozoic Solifugae (Arachnida) from the Cretaceous of Brazil, and a redescription of the Palaeozoic solifuge, 583
Semiotubina sakoi, 175
 Sennikov, A. G. See Gower, D. J. and Sennikov, A. G.
 Servais, T., Brocke, R. and Fatke, O. Variability in the Ordovician acritarch *Dicrodiaerodium*, 389
Shansisuchus shansisuchus, 893
 Sharks: Cretaceous, Australia, 813
 Shear, W. A. See Selden, P. A. and Shear, W. A.
 Shute, C. H. See Cleal, C. J., Laveine, J.-P. and Shute, C. H.
 Siliquariid gastropods, 157
 Silurian: brachiopods, 941; Chitinozoa, Ukraine, 629; dendroid graptolites, 219; spores, Silurian, England, 783; trigonotarbid arachnid, England, 605
 Siverson, M. Lamniform sharks of the Mid Cretaceous Alinga Formation and Beedagong Claystone, Western Australia, 813
 Smith, P. L. See Jakobs, G. K. and Smith, P. L.
 Smith R. M. H. and Evans, S. E. New material of *Youngina*: evidence of juvenile aggregation in Permian diapsid reptiles, 289
 Solifuges, 583
 South Africa: Permian diapsid reptiles, 289
 Spain: Devonian ammonoids, 149; Jurassic ammonoids, 851
Sphaerocoeloceras brochiforme, 142
Sphenothallus, 1037
Spirula, 694
 Spores: Jurassic, 724; Silurian, 783
Squalicorax ex gr. *curvatus*, 844; *S. volgensis*, 845
Stangerochampsia maccabei, 352

- Stemann, T. A. See Budd, A. F., Bosellini, F. R. and Stemann, T. A.
Steneosaurus manseli, 509; *S. palpebrosum*, 506
 Štorch, P. and Loydell, D. K. The Hirnantian graptolites *Normalograptus persculptus* and '*Glyptograptus*' *bohemicus*: stratigraphical consequences of their synonymy, 869
 Storrs, G. W., Gower, D. J. and Large, N. F. The diapsid reptile, *Pachystropheus rhaeticus*, a probable choristodere from the Rhaetian of Europe, 323
Strictocythere, 935
 Sudan: Cretaceous amphibians, 77
Supaia spp., 200
Sumeria galar, 858; *S. g. thieli*, 861; *S. nusplingensis*, 860; *S. platynota*, 856
 Swan, A. R. H. See Webb, L. P. and Swan, A. R. H.
 Symbiosis: Jurassic Foraminifera and photoautotrophs, 21
Synorisporites downtonensis, 784

T

- Taphonomy: Jurassic crocodile, 510
Tarbellastrea abdita, 540; *T. bragai*, 542; *T. carryensis*, 543; *T. chevalieri*, 543; *T. distans*, 544; *T. ellisiana*, 546; *T. profundata*, 548; *T. raulini*, 550; *T. reussiana*, 550; *T. russoi*, 552; *T. salentinensis*, 552; *T. tenera*, 553
 Temnospondyl amphibians: Triassic, Madagascar, 305
Thammasteria concinna, 413
Theobaldia circinalis, 11; *T. minor*, 11; *T. raetica*, 11
Tickalaracythere, 934
 Trace fossils: *Hehuinthopsis*, 1; *Theobaldia*, 11
 Triassic: archosaurs, 883; diapsid reptiles, 323, 883; Foraminifera, 44; palaeonisciform fish, England, 772; prolacertiform reptile, England, 763; temnospondyl amphibians, Madagascar, 305
 Trigonotarbids: Devonian, 611; Silurian, England, 605
 Trilobites: enrolment, 377; olenids, 377
Troglotella incrustans, 21
Tropidaster pectinatus, 182

U

- Ukraine: Silurian–Devonian Chitinozoa, 629
 Ultrastructure: Cretaceous spirulid coleoids, 681; Silurian spore masses, 783
 USA: Carboniferous solifuge, 583; Ordovician cnidarians, 1037; Ordovician conulariids, 1037; Ordovician *Sphenothallus*, 1037; Permian Capitan reef, 733

V

- Van Iten, H., Fitzke, J. A. and Cox, R. S. Problematical fossil cnidarians from the upper Ordovician of the north-central USA, 1037
- Vermetid gastropods, 157
- Vermicularia*, 173
- Vertebrates: body posture, 801; phylogeny, 259
- Vjushkovia triplicostata*, 884

W

- Wales: Ordovician bivalves, 979; Ordovician graptoloids, 869
- Walker, A. D. See Benton, M. J. and Walker, A. D.
- Wang Zi-qiang. Past global floristic changes: the Permian Great Eurasian Floral Interchange, 189
- Webb, L. P. and Swan, A. R. H. Estimation of parameters of foraminiferal test geometry by image analysis, 471
- Wellman, C. H. See Edwards, D., Davies, K. L., Richardson, J. B., Wellman, C. H. and Axe, L.
- Werner, C. See Evans, S. E., Milner, A. R. and Werner, C.
- Wetzel, A. and Bromley, R. G. Re-evaluation of the ichnogenus *Helminthopsis* – a new look at the type material, 1
- Whatley, R. C. and Ballent, S. A review of the Mesozoic ostracod genus *Progonocythere* and its close allies, 919

- Whittington, H. B. Sphaeroidal enrolment and thoracic characters in *Beltella depressa* and other olenid trilobites, 377
- Wilson, M. See Gagnier, P.-Y. and Wilson, M.
- Wood, R., Dixon, J. A. D. and Kirkland, B. L. New observations on the ecology of the Permian Capitan reef, Texas and New Mexico, 733
- Wright, A. D. and Rubel, M. A review of the morphological features affecting the classification of clitambonitidine brachiopods, 53
- Wright, J. K. Perisphinctid ammonites of the Upper Calcareous Grit (Upper Oxfordian) of North Yorkshire, 433
- Wu, X.-c. Brinkman, D. B. and Russell, A. P. A new alligator from the Upper Cretaceous of Canada and the relationships of early eusuchians, 351

X

- Xestoconcha* sp., 1009
- Xilousuchus sapingensis*, 891

Y

- Yakounia freboldi*, 133; *Y. pacifica*, 134; *Y. silvae*, 135; *Y. yakounensis*, 132
- Youngina*, 289

Z

- Zerqacythere*, 934
- Zhan, R.-b. See Rong, J.-y. and Zhan, R.-b.

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CONTENTS

	Part	Page
ALBERDI, M. T. See PRADO, J. L. and ALBERDI, M. T.		
AXE, L. See EDWARDS, D., DAVIES, K. L., RICHARDSON, J. B., WELLMAN, C. H. and AXE, L.		
BALLENT, S. See WHATLEY, R. C. and BALLENT, S.		
BENTON, M. J. See GRANGE, D. R. and BENTON, M. J.		
BENTON, M. J. and WALKER, A. D. <i>Rhombopholis</i> , a prolacertiform reptile from the Middle Triassic of England	3	765
BLAKE, D. B. Redescription and interpretation of the asteroid species <i>Tropidaster pectinatus</i> from the Jurassic of England	1	179
BOSELLINI, F. R. See BUDD, A. F., BOSELLINI, F. R. and STEMANN, T. A.		
BRAND, P. J. Taxonomy and distribution of the Upper Carboniferous non-marine bivalve <i>Carbonicola aldamii</i>	2	407
BRINKMAN, D. B. See WU, X.-C. BRINKMAN, D. B. and RUSSELL, A. P.		
BROCKE, R. See SERVAIS, T., BROCKE, R. and FATKE, O.		
BROMLEY, R. G. See WETZEL, A. and BROMLEY, R. G.		
BUDD, A. F., BOSELLINI, F. R. and STEMANN, T. A. Systematics of the Oligocene to Miocene reef coral <i>Tarbellastraea</i> in the northern Mediterranean region	3	515
BULL, E. E. Implications of normal and abnormal growth structures in a Scottish Silurian dendroid graptolite	1	219
CHRISTIAN, A. and PREUSCHOFT, H. Deducing the body posture of extinct large vertebrates from the shape of the vertebral column	4	801
CLEAL, C. J., LAVEINE, J.-P. and SHUTE, C. H. Architecture of the Upper Carboniferous pteridosperm frond <i>Macroneuropteris macrophylla</i>	3	561
COPE, J. C. W. Early Ordovician (Arenig) bivalves from the Llangynog Inlier, South Wales	4	979
COX, R. S. See VAN ITEN, H., FITZKE, J. A. and COX, R. S.		
CROMEY, J. A. A new oxytomid bivalve from the Upper Jurassic–Lower Cretaceous of Antarctica	3	615
DAVIES, K. L. See EDWARDS, D., DAVIES, K. L., RICHARDSON, J. B., WELLMAN, C. H. and AXE, L.		
DIXON, J. A. D. See WOOD, R., DIXON, J. A. D. and KIRKLAND, B. L.		
DOGUZHAeva, L. A. Two early Cretaceous spirulid coleoids of the north-western Caucasus: their shell ultrastructure and evolutionary implications	3	681
DUNLOP, J. A. A trigonotarbid arachnid from the Upper Silurian of Shropshire	3	605
DUTUIT, J.-M. See JALIL, N.-E. and DUTUIT, J.-M.		
EDWARDS, D., DAVIES, K. L., RICHARDSON, J. B., WELLMAN, C. H. and AXE, L. Ultrastructure of <i>Synorisporites downtouensis</i> and <i>Retusotriletes</i> cf. <i>coronatus</i> in spore masses from the Přídolí of the Welsh Borderland	3	785
EVANS, S. E. See SMITH, R. M. H. and EVANS, S. E.		
EVANS, S. E., MILNER, A. R. and WERNER, C. Sirenid salamanders and a gymnophionan amphibian from the Cretaceous of the Sudan	1	77
FARIÑA, R. A. See LESSA, E. P. and FARIÑA, R. A.		
FATKE, O. See SERVAIS, T., BROCKE, R. and FATKE, O.		
FITZKE, J. A. See VAN ITEN, H., FITZKE, J. A. and COX, R. S.		
GAGNIER, P.-Y. and WILSON, M. Early Devonian acanthodians from northern Canada	2	241
GARCÍA-ALCADE, J. L. See MONTESINOS, J. R. and GARCÍA-ALCADE, J. L.		
GOWER, D. J. See STORRS, G. W., GOWER, D. J. and LARGE, N. F.		
GOWER, D. J. and SENNIKOV, A. G. Morphology and phylogenetic informativeness of early archosaur braincases	4	883
GRAHN, Y. See PARIS, F. and GRAHN, Y.		
GRANGE, D. R. and BENTON, M. J. Kimmeridgian metriorhynchid crocodiles from England	2	497
HEWISON, R. H. The skull of <i>Deltacephalus whitei</i> , a lydekkerinid temnospondyl amphibian from the Lower Triassic of Madagascar	2	305

HORNÝ, R. J. See PEEL, J. S. and HORNÝ, R. J.		
INSALACO, E. The use of Late Jurassic coral growth bands as palaeoenvironmental indicators	2	413
JAKOBS, G. K. and SMITH, P. L. Latest Toarcian ammonoids from the North American Cordillera	1	97
JALIL, N.-E. and DUTUIT, J.-M. Permian captorhinid reptiles from the Argana formation, Morocco	4	907
JANVIER, P. The dawn of the vertebrates: characters versus common ascent in the rise of current vertebrate phylogenies	2	259
KIRKLAND, B. L. See WOOD, R., DIXON, J. A. D. and KIRKLAND, B. L.		
KNIGHT, R. I. and MORRIS, N. J. Inoceramid larval planktotrophy: evidence from the Gault Formation (Middle and basal Upper Albian), Folkestone, Kent	4	1027
KONIJNENBURG-VAN CITTERT, J. H. A. VAN. Two <i>Osmundopsis</i> species and their sterile foliage from the Middle Jurassic of Yorkshire	3	719
LARGE, N. F. See STORRS, G. W., GOWER, D. J. and LARGE, N. F.		
LAVEINE, J.-P. See CLEAL, C. J., LAVEINE, J.-P. and SHUTE, C. H.		
LEINFELDER, R. R. See SCHMID, D. U. and LEINFELDER, R. R.		
LESSA, E. P. and FARIÑA, R. A. Reassessment of extinction patterns among the Late Pleistocene mammals of South America	3	651
LOYDELL, D. K. See ŠTORCH, P. and LOYDELL, D. K.		
MILNER, A. R. See EVANS, S. E., MILNER, A. R. and WERNER, C.		
MONTESINOS, J. R. and GARCÍA-ALCADE, J. L. An occurrence of the auguritid ammonoid <i>Celaeceras</i> in the Lower Devonian of northern Spain	1	149
MORRIS, N. J. See KNIGHT, R. I. and MORRIS, N. J.		
NOTES FOR AUTHORS	4	1065
OLÓRIZ, F. and RODRÍGUEZ-TOVAR, F. J. The ammonite <i>Sutneria</i> from the Upper Jurassic of southern Spain	4	851
PARIS, F. and GRAHN, Y. Chitinozoa of the Silurian-Devonian boundary sections in Podolia, Ukraine	3	629
PEEL, J. S. and HORNÝ, R. J. Sinistral hyperstrophic coiling in a Devonian gastropod from Bohemia with an <i>in situ</i> operculum	3	709
PRADO, J. L. and ALBERDI, M. T. A cladistic analysis of the horses of the tribe Equini	3	663
PREUSCHOFT, H. See CHRISTIAN, A. and PREUSCHOFT, H.		
RICHARDSON, J. B. See EDWARDS, D., DAVIES, K. L., RICHARDSON, J. B., WELLMAN, C. H. and AXE, L.		
ROČEK, Z. The salamander <i>Brachycormus noachicus</i> from the Oligocene of Europe, and the role of neoteny in the evolution of salamanders	2	477
RODRÍGUEZ-TOVAR, F. J. See OLÓRIZ, F. and RODRÍGUEZ-TOVAR, F. J.		
RONG, J.-Y. and ZHAN, R.-B. Brachidia of Late Ordovician and Silurian eospiriferines (Brachiopoda) and the origin of the spiriferides	4	941
RUBEL, M. See WRIGHT, A. D. and RUBEL, M.		
RUSSELL, A. P. See WU, X.-C. BRINKMAN, D. B. and RUSSELL, A. P.		
SAVAZZI, E. Adaptations of vermetid and siliquarid gastropods	1	157
SCHMID, D. U. and LEINFELDER, R. R. The Jurassic <i>Lithocodium aggregatum-Troglotella incrustans</i> foraminiferal consortium	1	21
SELDEN, P. A. and SHEAR, W. A. The first Mesozoic Solifugae (Arachnida) from the Cretaceous of Brazil, and a redescription of the Palaeozoic solifuge	3	583
SENNIKOV, A. G. See GOWER, D. J. and SENNIKOV, A. G.		
SERVAIS, T., BROCKE, R. and FATKE, O. Variability in the Ordovician acritarch <i>Dicrodiaecrodium</i>	2	389
SHEAR, W. A. See SELDEN, P. A. and SHEAR, W. A.		
SHUTE, C. H. See CLEAL, C. J., LAVEINE, J.-P. and SHUTE, C. H.		
SIVERSON, M. Lamniform sharks of the Mid Cretaceous Alinga Formation and Beedagong Claystone, Western Australia	4	813
SMITH, P. L. See JAKOBS, G. K. and SMITH, P. L.		
SMITH R. M. H. and EVANS, S. E. New material of <i>Youngina</i> : evidence of juvenile aggregation in Permian diapsid reptiles	2	289

STEMANN, T. A. See BUDD, A. F., BOSELLINI, F. R. and STEMANN, T. A.		
ŠTORCH, P. and LOYDELL, D. K. The Hirnantian graptolites <i>Normalograptus persculptus</i> and ' <i>Glyptograptus bohemicus</i> : stratigraphical consequences of their synonymy	4	869
STORRS, G. W., GOWER, D. J. and LARGE, N. F. The diapsid reptile, <i>Pachystropheus rhaeticus</i> , a probable choristodere from the Rhaetian of Europe	2	323
SWAN, A. R. H. See WEBB, L. P. and SWAN, A. R. H.		
VAN ITEN, H., FITZKE, J. A. and COX, R. S. Problematical fossil cnidarians from the upper Ordovician of the north-central USA	4	1037
WALKER, A. D. See BENTON, M. J. and WALKER, A. D.		
WANG ZI-QIANG. Past global floristic changes: the Permian Great Eurasian Floral Interchange	1	189
WEBB, L. P. and SWAN, A. R. H. Estimation of parameters of foraminiferal test geometry by image analysis	2	471
WELLMAN, C. H. See EDWARDS, D., DAVIES, K. L., RICHARDSON, J. B., WELLMAN, C. H. and AXE, L.		
WERNER, C. See EVANS, S. E., MILNER, A. R. and WERNER, C.		
WETZEL, A. and BROMLEY, R. G. Re-evaluation of the ichnogenus <i>Helminthopsis</i> – a new look at the type material	1	1
WHATLEY, R. C. and BALLENT, S. A review of the Mesozoic ostracod genus <i>Progonocythere</i> and its close allies	4	919
WHITTINGTON, H. B. Sphaeroidal enrolment and thoracic characters in <i>Beltella depressa</i> and other olenid trilobites	2	377
WILSON, M. See GAGNIER, P.-Y. and WILSON, M.		
WOOD, R., DIXON, J. A. D. and KIRKLAND, B. L. New observations on the ecology of the Permian Capitan reef, Texas and New Mexico	3	733
WRIGHT, A. D. and RUBEL, M. A review of the morphological features affecting the classification of clitambonitidine brachiopods	1	53
WRIGHT, J. K. Perisphinctid ammonites of the Upper Calcareous Grit (Upper Oxfordian) of North Yorkshire	2	433
WU, X.-C. BRINKMAN, D. B. and RUSSELL, A. P. A new alligator from the Upper Cretaceous of Canada and the relationships of early eusuchians	2	351
ZHAN, R.-B. See RONG, J.-Y. and ZHAN, R.-B.		

NOTES FOR AUTHORS

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Palaeontology

VOLUME 39 · PART 4

CONTENTS

Deducing the body posture of extinct large vertebrates from the shape of the vertebral column ANDREAS CHRISTIAN <i>and</i> HOLGER PREUSCHOF	801
Lamniform sharks of the Mid Cretaceous Alinga Formation and Beedagong Claystone, Western Australia MIKAEL SILVERSON	813
The ammonite <i>Sutneria</i> from the Upper Jurassic of southern Spain F. OLÓRIZ <i>and</i> F. J. RODRÍGUEZ-TOVAR	851
The Hirnantian graptolites <i>Normalograptus persculptus</i> and ' <i>Glyptograptus</i> ' <i>bohemicus</i> : stratigraphical consequences of their synonymy PETR ŠTORCH <i>and</i> DAVID K. LOYDELL	869
Morphology and phylogenetic informativeness of early archosaur braincases D. J. GOWER <i>and</i> A. G. SENNIKOV	883
Permian captorhinid reptiles from the Argana Formation, Morocco NOR-EDDINE JALIL <i>and</i> JEAN-MICHEL DUTUIT	907
A review of the Mesozoic ostracod genus <i>Progonocythere</i> and its close allies R. C. WHATLEY <i>and</i> S. BALLENT	919
Brachidia of Late Ordovician and Silurian eospiriferines (Brachiopoda) and the origin of the spiriferides RONG JIA-YU <i>and</i> ZHAN REN-BIN	941
Early Ordovician (Arenig) bivalves from the Llangynog Inlier, South Wales JOHN C. W. COPE	979
Inoceramid larval planktotrophy: evidence from the Gault Formation (Middle and basal Upper Albian), Folkestone, Kent R. I. KNIGHT <i>and</i> N. J. MORRIS	1027
Problematical fossil cnidarians from the upper Ordovician of the north-central USA HEYO VAN ITEN, JULIE ANN FITZKE <i>and</i> ROBT S. COX	1037
Notes for authors THE EDITORS	1065

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